

# Bonn zoological Bulletin

Volume 68  
Issue 2  
2019

formerly: Bonner zoologische Beiträge



An open access journal of organismal zoology, published by  
Zoologisches Forschungsmuseum Alexander Koenig, Bonn

BHL



Blank Page Digitally Inserted



## Research article

urn:lsid:zoobank.org:pub:F0246630-F65F-4FF1-BF4E-008D483BDA2C

# *Euophrys petrensis* C. L. Koch, 1837 is a genuine member of the genus *Talavera* (Araneae: Salticidae)

**Rainer Breitling**

*Faculty of Science and Engineering, University of Manchester, Manchester M1 7DN, UK*

*\*Corresponding author: Email: [rainer.breitling@manchester.ac.uk](mailto:rainer.breitling@manchester.ac.uk)*

urn:lsid:zoobank.org:author:17A3B585-0E06-436C-A99A-1C7F24DC88D7

**Abstract.** The small jumping spider *Euophrys petrensis* C. L. Koch, 1837 combines morphological characters of both *Euophrys* s. str. and *Talavera*, and its generic placement has consequently been contentious. After many years of being placed in *Talavera*, the species has recently been transferred back to *Euophrys*. Here, public DNA barcoding data are used to confirm that the species should be placed in the genus *Talavera*, as *T. petrensis*, **stat. rev.**, as is also indicated by several putative morphological synapomorphies identified earlier.

**Key words.** Araneae, DNA barcoding, phylogenetic systematics.

## INTRODUCTION

The taxonomic placement of *Euophrys petrensis* has been problematic for some time, since the revision and major expansion of the genus *Talavera* Peckham & Peckham, 1909, by Logunov (1992). Logunov (1992) transferred four Palearctic members of *Euophrys* s. lat. to *Talavera* (*T. aequipes*, *T. monticola*, *T. thorelli*, and *T. trivittata*). However, he delayed the transfer of their close relative, *E. petrensis*, as the latter showed ambiguous characters implying a possible closer affinity to *Euophrys* s. str. (e.g., chitinous rings in the epigynum and twisted insemination ducts, as well as a pronounced sexual dimorphism). Logunov (1992) also remarked that *T. aequipes* occupies a similar morphologically intermediate position between *Talavera* and *Euophrys* s. str.

Logunov et al. (1993) then indicated that all species of their *petrensis* group of *Euophrys* s. lat. (*E. petrensis*, *E. aequipes*, and *E. thorelli*) should be included in the genus *Talavera*, without, however, providing additional arguments regarding *E. petrensis* itself.

The transfer of the latter was formalized by Żabka (1997; see also Żabka & Prószyński 1998), and *Talavera petrensis* was generally accepted as the valid combination by subsequent authors. Logunov & Kronstedt (2003) reviewed *Talavera* s. lat. and list the diagnostic characters of the expanded genus: absence of a tibial apophysis; endite tooth on the male maxilla; long white/red hairs on the base of the cymbium; clearly exposed embolus-tegulum membrane; thin, thread-like insemination ducts; and scales with a well-marked keel on carapace and abdomen.

However, most recently, Prószyński et al. (2018) transferred *T. petrensis* back to *Euophrys*, but maintained

other members of the *petrensis* group (sensu Logunov et al. 1993), such as *T. aequipes* and *T. thorelli*, within *Talavera*. This re-transfer was based on Prószyński's non-cladistic approach combined with a different relative weighting of the various characters already highlighted as ambiguous by Logunov (1992): the coiled embolus and colourful frontal hairs of the male. The absence of a tibial apophysis, which Logunov & Kronstedt (2003) describe as one of the most important diagnostic characters of *Talavera*, was considered as non-informative, as the apophysis in *Euophrys* s. str. is typically highly reduced, and the thin copulatory ducts were considered an artefact of observation by optical microscopy, while “they appear much broader” when observed by scanning electron microscopy (Prószyński et al. 2018); this latter argument is not quite convincing, being based on a rather subjective comparison of published figures. The other characters discussed by Logunov & Kronstedt (2003) received no further attention.

Given this controversial history, it was interesting to examine if the publicly available barcoding sequences could be used to supplement the morphological data to resolve the placement of *Euophrys petrensis*, in analogy to the approach taken in Breitling (2017, 2019). In a barcoding study of German spiders, the species had already been shown as sister of *Talavera aequipes*, rather than *Euophrys frontalis* (Astrin et al. 2016: Supplementary Figures S1 and S2); as these results were based on a limited set of species and were not further discussed in the article, the robustness of this relationship remained unclear, but the results certainly indicated that the barcode data should contain relevant phylogenetic information.



## MATERIAL AND METHODS

All public Cytochrome Oxidase Subunit 1 5' region barcodes (COI-5P) for members of *Euophrys*, *Talavera* and *Pseudeuophrys* (i.e. *Euophrys* s. lat.), and the closely related genus *Chalcoscirtus* were downloaded in FASTA format from the BOLD database (www.boldsystems.org; Ratnasingham & Hebert 2007) in April 2018. Sequences were aligned in BioEdit v7.2.5 (Hall 1999), and trailing gaps and particularly short sequences were removed to maximize the amount of sequence positions for which all specimens in the analysis had data available. The resulting dataset included 540 residues of the COI-5P barcode for 59 specimens. The BOLD and GenBank accession numbers of all sequences in the final dataset are shown in Figure 1.

The data included barcode sequences for four species of *Talavera* (13 specimens of the type species, *T. minuta*, two specimens of *T. petrensis* and one specimen each of *T. thorelli* and *T. aequipes*). Together, these four species represent all four species groups of *Talavera* s. lat. defined by Logunov & Kronstedt (2003). Also included in the dataset are representatives of *Euophrys* s. str. (17 specimens of the type species, *E. frontalis*, and five of *E. monadnock*), of *Pseudeuophrys* (seven specimens of the type species, *P. erratica*, six specimens of *P. lanigera*, and two of *P. obsoleta*), and two species of *Chalcoscirtus* (two specimens of *C. alpicola*, and three of *C. carbonarius*), which in preliminary analyses of salticid barcodes were consistently nested within *Euophrys* (Breitling 2019).

The plausibility of the identification of the *T. petrensis* specimens critical for this analysis was confirmed using the data deposited in BOLD: the material was collected in Saxony-Anhalt, well within the known range of the species (which extends from Ireland to Central Asia and from Finland to the Mediterranean), identified by Karl-Hinrich Kielhorn, an experienced arachnologist, and is deposited in the Zoologische Staatssammlung München. Both specimens are adult males, which are particularly easy to identify reliably, and the habitus photographs available in BOLD further support the identification.

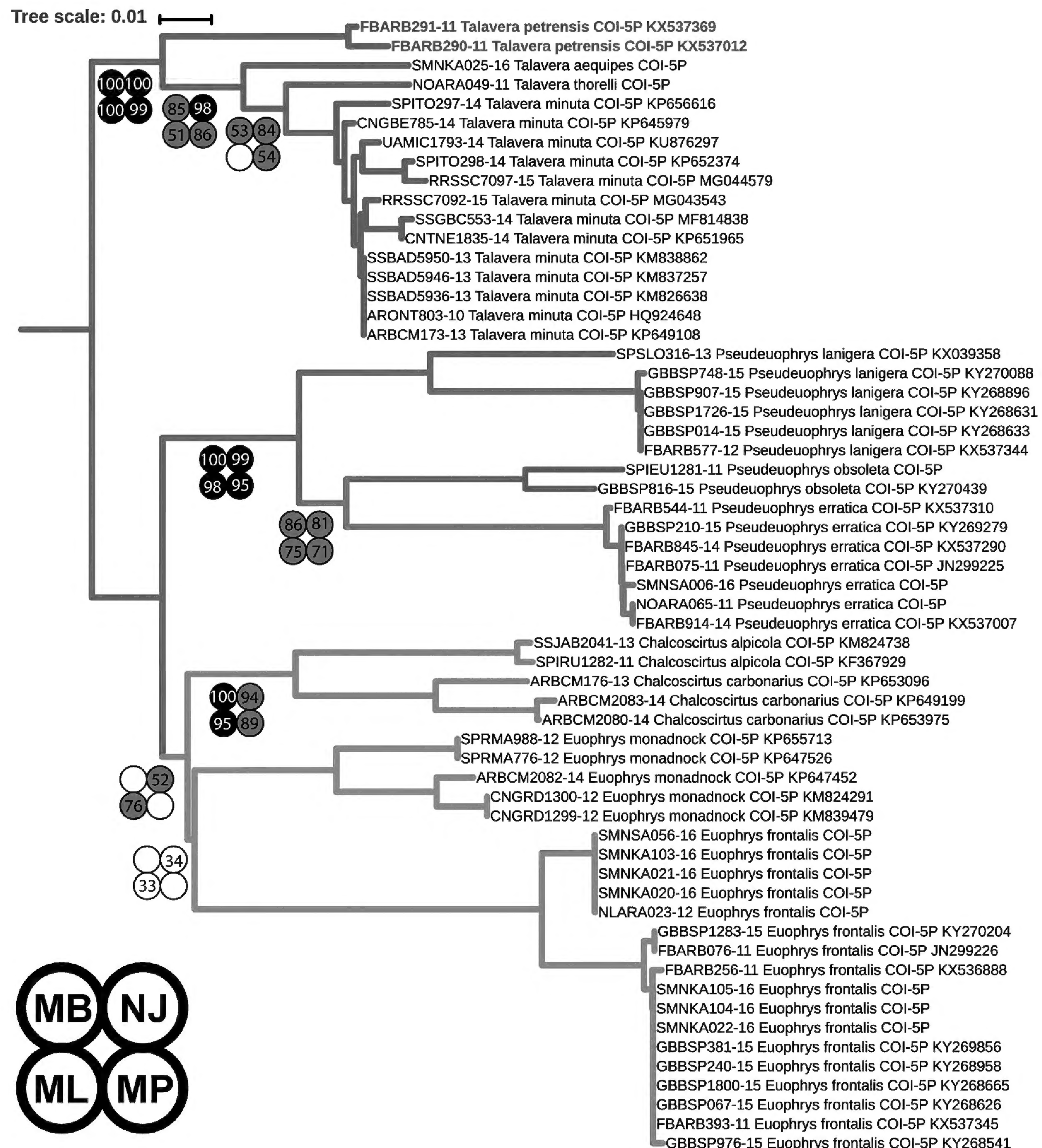
Phylogenetic trees were reconstructed using phylogeny.fr (Dereeper et al. 2008) as described in Breitling (2017), using the default workflow and parameters to infer Maximum Likelihood (PhyML 3.1; Guindon & Gascuel 2003), Maximum Parsimony (TNT 1.1; Goloboff et al. 2008) and Bayesian trees (MrBayes 3.2.6; Ronquist & Huelsenbeck 2003). Sequences were not partitioned by codon for the analysis. For the Bayesian analysis, the standard (4by4) model of nucleotide substitution was used, while the rate variation across sites was set to “invgamma”. Four Markov Chain Monte Carlo chains were run for 100 000 generations, sampling every 100 generations, with the first 1000 sampled trees discarded as “burn-in”. Finally, a 50% majority rule consensus tree

was constructed. For the Maximum Likelihood analysis, the default substitution model was selected assuming an estimated proportion of invariant sites (of 0.577) and 4 gamma-distributed rate categories to account for rate heterogeneity across sites. The gamma shape parameter was estimated directly from the data (gamma=1.268). Branch support values are based on an Approximate Likelihood-Ratio Test (aLRT; Anisimova & Gascuel 2006) for the Maximum Likelihood results, on 1000 bootstrap replicates for the Maximum Parsimony and Neighbour Joining results, and on posterior probabilities for the Bayesian analysis. Trees were visualized using iTOL (Letunic & Bork 2016) and annotated in Adobe Illustrator.

## RESULTS & DISCUSSION

The barcoding data provide unambiguous support for the placement of *Euophrys petrensis* C. L. Koch, 1837, in the genus *Talavera*, as *T. petrensis*, **stat. rev.** The *maximum* interspecies distance between barcodes within the genus *Talavera* is 8.5% (between one of the *T. petrensis* specimens and *T. aequipes*). In contrast, the *minimum* distance between *Talavera* and any member of *Euophrys* is 11.4% (between one of the *T. petrensis* specimens and one specimen of *E. monadnock*). The minimum distance between *T. petrensis* and the type species of *Euophrys*, *E. frontalis*, is 12.2%, and the closest member of *Pseudeuophrys* (*P. obsoleta*) has a distance of 12.9%. This is clearly a much larger barcoding distance, especially when considering that, on average, barcode sequences for species assigned to the same genus differ by 10.5% among Salticidae in the BOLD database, and the numbers are even lower for other families (e.g., 10.0% for Thomisidae, 8.5% for Theridiidae, and 6.2% for Lycosidae; Breitling, unpubl. data). To give a sense of the scale of this difference: of the 72 base pairs shared between *T. petrensis* and either *T. minuta* or *E. frontalis* (but not both), 16 are shared with *E. frontalis*, and 56 with *T. minuta*. Assuming a uniform mutation rate (as would appear reasonable for such a closely related group), this finding is obviously not compatible with a closer relationship between *T. petrensis* and *E. frontalis*. Consequently, all the tree reconstruction methods recover a monophyletic genus *Talavera*, including *T. petrensis*, with strong bootstrap and posterior probability support (99% bootstrap support in the Maximum Parsimony tree, 100% bootstrap support in the Neighbour Joining analysis, 100% posterior probability in the Bayesian analysis, and 100% approximate LRT in the Maximum Likelihood tree), and almost always with the same internal topology (*T. petrensis* as sister to the other three species), as shown in Figure 1. The corresponding node is the most strongly supported interspecific node in the entire tree, with higher support values than the also highly supported node joining the three *Pseudeuophrys* species. None of the trees indicates a closer relationship





**Fig. 1.** DNA-Barcode-based tree of *Talavera* and its relatives. The topology and branch lengths are based on the Neighbour Joining tree. The genus *Talavera* forms a very strongly supported monophyletic group, including *T. petrensis*, in all four tree reconstructions, but its relationships to the other members of *Euophrys* s. lat. are not convincingly resolved in the dataset. Black circles indicate more than 95% posterior probability (MB), approximate likelihood (ML), or bootstrap support (MP, NJ); grey circles indicate support values between 50% and 95%. White circles indicate branches that were either not recovered or had a support below 50%. Support values for intraspecific branches are not shown (all species were recovered as monophyletic in all analyses).

of *T. petrensis* to *Euophrys* s. str. or *Pseudeuophrys* with any degree of support. This result is consistent with the barcode-based trees of German spider species shown in the Supplementary Material of Astrin et al. (2016).

As expected, the details of the relationship between *Talavera*, *Euophrys* s. str. and *Pseudeuophrys* are not unambiguously resolved by the barcode data. In the Bayesian and Maximum Likelihood analyses there is some

evidence that the three genera are part of a (monophyletic) clade (*Euophrys* s. lat.), as would be expected on the basis of their morphological similarity, and *Pseudeuophrys* is consistently recovered as monophyletic as well in all analyses. The diversity of *Euophrys* s. str. is not sufficiently represented to assess its monophyly, and its relationship with *Chalcoscirtus* is not convincingly resolved. In several of the reconstructed trees, *Chalco-*



*scirtus* is nested within a paraphyletic *Euophrys* s. str. As *Chalcoscirtus* appears to be represented only by female specimens in the database, it is not impossible that this finding is due to a misidentification. But, as the case involves multiple specimens from several locations, including material identified by an experienced arachnologist, Gergin Blagoev, the possibility that *Chalcoscirtus* forms a highly derived monophyletic subgroup within a paraphyletic *Euophrys* s. str. as presently defined cannot be discarded outright. The genus *Chalcoscirtus* is defined by a number of characteristic synapomorphies, such as the dark, strongly sclerotized, glabrous prosoma, the male opisthosomal scutum and the absence of retromarginal cheliceral teeth (Cutler 1990). Its key diagnostic character is the presence of a ventral tibial apophysis, but the absence of this apophysis in *Euophrys* is a symplesiomorphy, shared with *Pseudeuophrys* and *Talavera*. Thus, there are currently no convincing synapomorphies for *Euophrys* s. str., and the genitalia of the two genera are obviously very similar in both sexes. Of course, it would also be possible that *Chalcoscirtus* is polyphyletic, and that the two species in the dataset are not closely related to *Chalcoscirtus* s. str., i.e., *C. infimus* and its mostly Central Asian close relatives. However, the large number of convincing synapomorphies supporting the genus makes this hypothesis much less plausible.

It is striking that the barcoding data allow such a clear assignment of “*Euophrys*” *petrensis* to the genus *Talavera*. The ambiguous morphological data had indicated a more “intermediate” position, i.e., a trichotomy or very shallow branching between *Euophrys*, *Talavera* s. str. and *T. petrensis*, which could have been reflected in a much smaller (or non-existent) difference in barcoding distance and possibly an unresolved or ambiguous placement of *T. petrensis* in the various phylogenetic reconstructions. The molecular evidence can stimulate a renewed look at the morphological data as well. It appears that the absence of a tibial apophysis, presence of an endite tooth on the maxilla, exposed embolus–tegulum membrane, long red and white hairs at the base of the cymbium, and keeled scales are indeed synapomorphies of *Talavera* (and, in the case of the missing tibial apophysis, its supposed sister group *Tanzania*; Logunov & Kronstedt 2003, sub *Lilliput*), while the coiled embolus, relatively thick and twisted insemination duct, and pronounced sexual dimorphism, including colourful cymbial setae, are possible symplesiomorphies maintained in the basal *T. petrensis*, and shared with, e.g., *Euophrys*, but lost in the other *Talavera* species, as already suggested by Logunov (1992). More derived *Talavera* species (beyond the *petrensis* and *aequipes* group) are then additionally characterized by a number of derived characters of the male pedipalp (e.g., a more complex sperm duct, a chitinous ligament connecting the embolus and the tegulum, and a distal tegular sclerite; Logunov & Kronstedt 2003).

Of course, the fact that we have been able to refute one of the two alternative hypotheses that we began with does not necessarily mean that the other hypothesis is correct. Thus, while the barcode data do not provide any reason to doubt the taxonomic placement suggested by Logunov & Kronstedt (2003), future studies may well change this assessment. Additional analyses, using larger datasets, will also be required to determine the precise relationships between the various Euophryine genera, including *Chalcoscirtus*. The success of barcode information in suggesting an unambiguous solution to the taxonomic conundrum regarding the generic placement of *Talavera petrensis* should encourage the further use of public barcoding databases as a valuable resource to complement morphological approaches to spider taxonomy, especially in cases where morphological analysis has resulted in ambiguous or controversial placements.

**Acknowledgements.** I thank Jonas Astrin, Dmitri Logunov, Wayne Maddison, Junxia Zhang and an anonymous referee for their detailed and critical comments on the manuscript, which have helped improving the argument considerably.

## REFERENCES

- Anisimova M, Gascuel O (2006) Approximate likelihood-ratio test for branches: A fast, accurate, and powerful alternative. *Systematic Biology* 55(4): 539–552
- Astrin JJ, Höfer H, Spelda J, Holstein J, Bayer S, Hendrich L, Huber BA, Kielhorn KH, Krammer HJ, Lemke M, Monje JC, Morinière J, Rulik B, Petersen M, Janssen H, Muster C (2016) Towards a DNA barcode reference database for spiders and harvestmen of Germany. *PLoS ONE* 11 (e0162624): 1–24. <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0162624>
- Breitling R (2017) Public DNA barcoding data resolve the status of the genus *Arboricaria* (Araneae: Gnaphosidae). *Arachnologische Mitteilungen* 54: 24–27. <https://arages.de/105431/aramit5405>
- Breitling R (2019) Barcode taxonomy at the genus level. *Ecologica Montenegrina* 21: 17–37
- Cutler B 1990 A revision of the western hemisphere *Chalcoscirtus* (Araneae: Salticidae). *Bulletin of the British Arachnological Society* 8: 105–108
- Dereeper A, Guignon V, Blanc G, Audic S, Buffet S, Chevenet F, Dufayard JF, Guindon S, Lefort V, Lescot M, Claverie JM, Gascuel O (2008) Phylogeny.fr: robust phylogenetic analysis for the non-specialist. *Nucleic Acids Research* 36 (Web Server issue): W465–W469. <https://www.ncbi.nlm.nih.gov/pubmed/18424797>
- Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786. <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1096-0031.2008.00217.x>
- Guindon S, Gascuel O (2003) A simple, fast and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52: 696–704. doi: <https://doi.org/10.1080/10635150390235520>
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98



- Letunic I, Bork P (2016) Interactive tree of life (iTOL) v3: an online tool for the display and annotation of phylogenetic and other trees. *Nucleic Acids Research* 44: W242–W245. <https://www.ncbi.nlm.nih.gov/pubmed/27095192>
- Logunov DV (1992) Definition of the spider genus *Talavera* (Araneae, Salticidae), with a description of a new species. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique (Ent.)* 62: 75–82
- Logunov DV, Cutler B, Marusik YM (1993) A review of the genus *Euophrys* C. L. Koch in Siberia and the Russian Far East (Araneae: Salticidae). *Annales Zoologici Fennici* 30: 101–124
- Logunov DV, Kronstedt T (2003) A review of the genus *Talavera* Peckham and Peckham, 1909 (Araneae, Salticidae). *Journal of Natural History* 37: 1091–1154
- Prószyński J, Lissner J, Schäfer M (2018) Taxonomic survey of the genera *Euophrys*, *Pseudeuophrys* and *Talavera*, with description of *Euochin* gen. n. (Araneae: Salticidae) and with proposals of a new research protocol. *Ecologica Montenegrina* 18: 26–74
- Ratnasingham S, Hebert PDN (2007) BOLD: The Barcode of Life Data system ([www.barcodinglife.org](http://www.barcodinglife.org)). *Molecular Ecology Notes* 7: 355–364. <https://onlinelibrary.wiley.com/doi/full/10.1111/j.1471-8286.2007.01678.x>
- R Core Team (2018) R: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19 (12): 1572–1574
- Wright ES (2016) Using DECIPHER v2.0 to Analyze Big Biological Sequence Data in R. *The R Journal* 8 (1): 352–359
- Żabka M (1997) Salticidae: Pająki skaczące (Arachnida: Araneae). *Fauna Polski* 19: 1–188
- Żabka M, Prószyński J (1998) Middle European *Euophrys* C. L. Koch, 1834 (Araneae: Salticidae) – one, two or three genera? In: Selden PA (ed.) *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997*. Edinburgh, pp. 115–120



BHL



Blank Page Digitally Inserted



## Research article

urn:lsid:zoobank.org:pub:7EF7A263-F535-43F7-B6E5-94012D1CE048

# The *Knautia* feeding species of *Aphis* (Insecta: Hemiptera: Aphididae) with notes on *Aphis knautiae* Holman nomen nudum

Mariusz Kanturski<sup>1,\*</sup> & Aleš Bezděk<sup>2</sup>

<sup>1</sup>Department of Zoology, Faculty of Biology and Environmental Protection, University of Silesia in Katowice, Bankowa 9, PL-40-007 Katowice, Poland

<sup>2</sup>Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Branišovská 1160/31, CZ-370 05 České Budějovice, Czech Republic

\*Corresponding author: Email: [mariusz.kanturski@us.edu.pl](mailto:mariusz.kanturski@us.edu.pl)

<sup>1</sup>urn:lsid:zoobank.org:author:78C290A3-D07B-4AF9-9358-ED8C05A702BF

<sup>2</sup>urn:lsid:zoobank.org:author:E7A39AC2-AE8C-4CF1-8594-7951FF5A7058

**Abstract.** Here we present a review of *Knautia* feeding aphid species of the genus *Aphis* Linnaeus, 1758 (Insecta: Hemiptera: Aphididae). A new European species *Aphis holmani* sp. nov. is described from specimens collected in the Czech Republic, Bulgaria and Romania by the late Jaroslav Holman, who already recognized this new species, but never published its description. It has previously been referred to as *Aphis knautiae* Holman nomen nudum. Morphological characters of apterous and alate viviparous females as well as the sexual generation (oviparous females and males) are described and figured. The new species is associated with *Knautia drymeia* and its affinities with other related species living on species of *Knautia* are presented. Morphological characteristics of known morphs of other *Knautia* feeding species *A. confusa* Walker, 1849, *A. longini* Huculak, 1968 and *A. thomasi* (Börner, 1950) are given and figured. Additionally hitherto unknown sexual forms of *A. thomasi* are described from specimens collected in the Czech Republic and Poland. A key to known aphid species living on species of *Knautia* is also provided.

**Key words.** Aphidini, Aphidoidea, description, Europe, taxonomy, *Aphis holmani* sp. nov.

## INTRODUCTION

*Aphis* Linnaeus, 1758 with 589 valid species is the most speciose genus within the Aphidoidea as a whole (Favret 2019; Blackman & Eastop 2019). Species belonging to this genus are known mostly from the northern hemisphere with small number of taxa which are native for the southern part of the globe. Most of species form groups of similar or very similar species whose elucidation may be difficult, but mostly all they are characterized by terminal process which is no longer than the fourfold of the basal part length, relatively short siphunculi and a subtriangular or tongue-shaped cauda. Viviparous and sexual generations of *Aphis* are furthermore characterized by undeveloped or low antennal tubercles with a little convex frons, marginal tubercles on prothorax, abdominal segments I and VII and occasionally on other segments of the abdomen, which although lack in some species (Heie 1986).

The plant genus *Knautia* L. (Dipsacaceae) comprises about 50–55 species distributed in western Eurasia and northwestern Africa, with the highest species diversity is in southern and southeastern Europe, especially the Alps and the Balkan Peninsula. Species from this genus can be found dry grasslands, wet meadows, alpine grasslands,

forests, and ruderal communities (Ehrendorfer 1976; Rešetnik et al. 2014). So far 11 aphids species have been described or recorded from ten *Knautia* species of which three species belong to genus *Aphis*: *A. confusa* Walker, 1849, *A. longini* Huculak, 1968 and *A. thomasi* (Börner, 1950) are associated with *Knautia arvensis* (L.) Coult., *K. dinarica* (Murb.) Borbás, *K. dipsacifolia* Kreutzer and *K. integrifolia* Ehrend. Only *A. confusa* feeds on all four species (both, *A. longini* and *A. thomasi* are known only from *K. arvensis*) (Holman 2009; Blackman & Eastop 2019).

*Knautia drymeia* Heuff. has a native distribution range from South-eastern Germany to Northern Greece (Albania, Austria, Bulgaria, Czech Republic, Croatia, Greece, Hungary, Montenegro, Romania, Serbia and Slovakia) (Rešetnik et al. 2016). It is a perennial herb, usually with a monopodial stalk bearing a terminal leaf rosette and lateral flowering stems. Its habitats are forests and forest margins, especially deciduous and hard-wood floodplain forests, but it also reaches into subalpine habitats (Ehrendorfer 1962; Fischer et al. 2008). Only four aphid species from the tribe Macrosiphini have been reported from this species to date: *Aulacorthum knautiae* Heie, 1960, *Macrosiphum knautiae* Holman, 1972, *M. rosae* (Linnaeus,



1758) and *Ovatomyzus boraginacearum* Eastop, 1952 (Holman 2009).

Another nominal species associated with *K. drymeia* is *Aphis knautiae* Holman which was for the first time mentioned in 1981 in the list of aphids of Romania (Holman & Pintera 1981) but recognized as a nomen nudum (ICZN 1999; Remaudière & Remaudière 1997; Favret 2019). During the work in the Aphidoidea collection of the late Jaroslav Holman (now deposited in the Biology Centre of the Czech Academy of Sciences, Institute of Entomology, České Budějovice, Czech Republic) specimens collected in the Czech Republic, Bulgaria and Romania from *K. drymeia* and labeled as “*Aphis knautiae* Holman” have been found and recognized as *A. knautiae* Holman nomen nudum. A careful examination and comparison with other *Aphis* species associated with *Knautia* revealed that the specimens represent an undescribed species; its diagnosis and detailed description is given in this paper which makes this name available.

## MATERIAL AND METHODS

The specimens were examined using light microscope Leica DM 3000 led with Leica MC 190 HD camera and Nikon Eclipse E600 with Nikon DS-Fi camera. The measurements were done according to Ilharco & van Harten (1987) and Blackman & Eastop (2006). Measurements are given in millimeters (Supplementary tables 1–4).

### Abbreviations

ANT	= antennae or their lengths
ANT I–VI	= antennal segments I, II, III, IV, V, VI or their lengths (ratios between antennal segments are simply given as e.g. ‘VI: III’)
BASE	= basal part of last antennal segment or its length
BD III	= basal articular diameter of ANT III
BL	= body length (from anterior border of the head to the end of cauda)
FEMORA III	= hind femora length
FEMORA III LS	= longest setae on hind femora
GP	= genital plate
PHT	= posterior seta (hair) of hind trochanter
HW	= greatest head width across compound eyes
HT II	= second segment of hind tarsus or its length
LS ANT III	= length of longest setae of ANT III
MAX W	= maximal width of abdomen
PT	= processus terminalis of last antennal segment or its length
MTu	= marginal tubercles

SIPH L	= siphunculi length
SIPH W	= maximum width of siphunculus
TIBIAE III	= hind tibiae length
URS	= ultimate segments of rostrum (IV + V) or their length
apt.	= apterous viviparous female
al.	= alate viviparous female
♀	= oviparous female
♂	= male

### Depositories of the material examined

- DZUS** = Hemiptera Collection of the Department of Zoology, University of Silesia in Katowice, Poland
- IECA** = Biology Centre of the Czech Academy of Sciences, Institute of Entomology, České Budějovice, Czech Republic;
- ZMPA** = Zoological Institute, Polish Academy of Sciences, Warsaw, Poland

## RESULTS

### Shared characters of *Aphis* species feeding on *Knautia* spp.

Body egg or pear-shaped. Head slightly sclerotized with very small and slightly visible ANT tubercles and sub-convex frons. Head and body sclerotization often with microsculpture. ANT 5 or 6-segmented. ANT III without secondary rhinaria, ANT V with small ciliated rhinarium. ANT VI with small ciliated major rhinarium, 5–6 visible additional rhinaria and 4 apical setae. Ultimate rostral segment with 2 (sometimes 4) accessory setae. First segments of tarsi with 3–3–2 ventral setae. Dorsum of thorax membranous, sometimes with more or less visible sclerotic plates on marginal areas. Dorsum of thorax and abdomen covered by a few short, rigid setae with blunt apices. Abdomen membranous. ABD I and VII always with MTu. Siphunculi short, cylindrical, slightly tapering. Cauda short, tongue-shaped. Alate viviparous females with small number of secondary rhinaria on ANT III and IV. Abdomen with marginal sclerotic plates on ABD II–IV. ABD VI with wide postsiphuncular sclerites. Oviparous females with more or less swollen hind tibiae with rounded or slightly oval pseudosensoria on almost whole length and genital plate divided into two separated sclerotic parts. Males apterous with small number of secondary rhinaria on ANT III–V. They are small, rounded with sclerotic rings. Male genitalia with wide and lobate parameres with a large number of long and pointed setae. Basal part of the phallus short and hooked-shaped.



### Morphological characteristics of species

#### *Aphis (Aphis) confusa* Walker, 1849

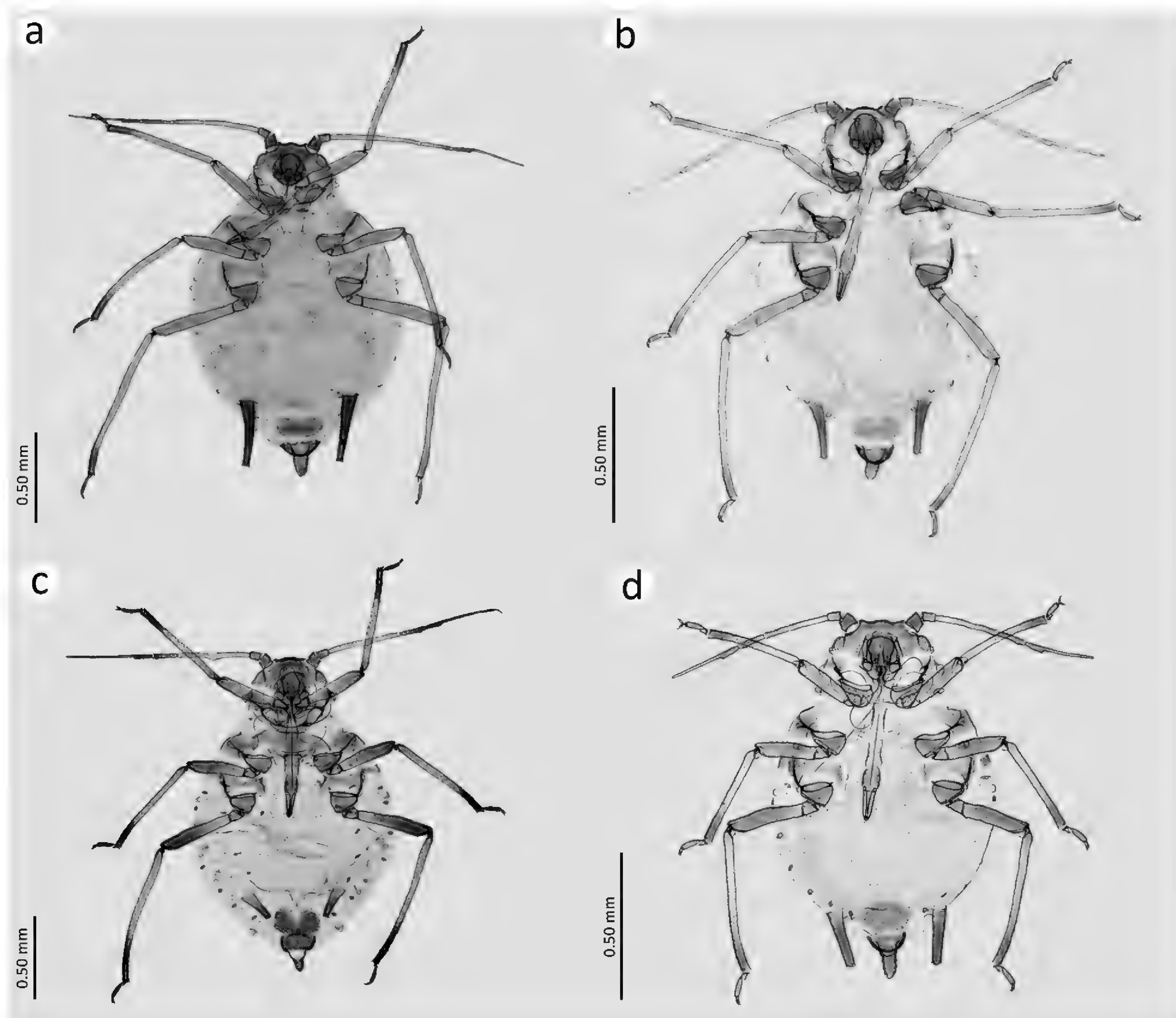
Walker, 1849: XLV

Figs 1–7; Supplementary tables 1–4; Tables 1–2

#### *Apterous viviparous female* (n=27).

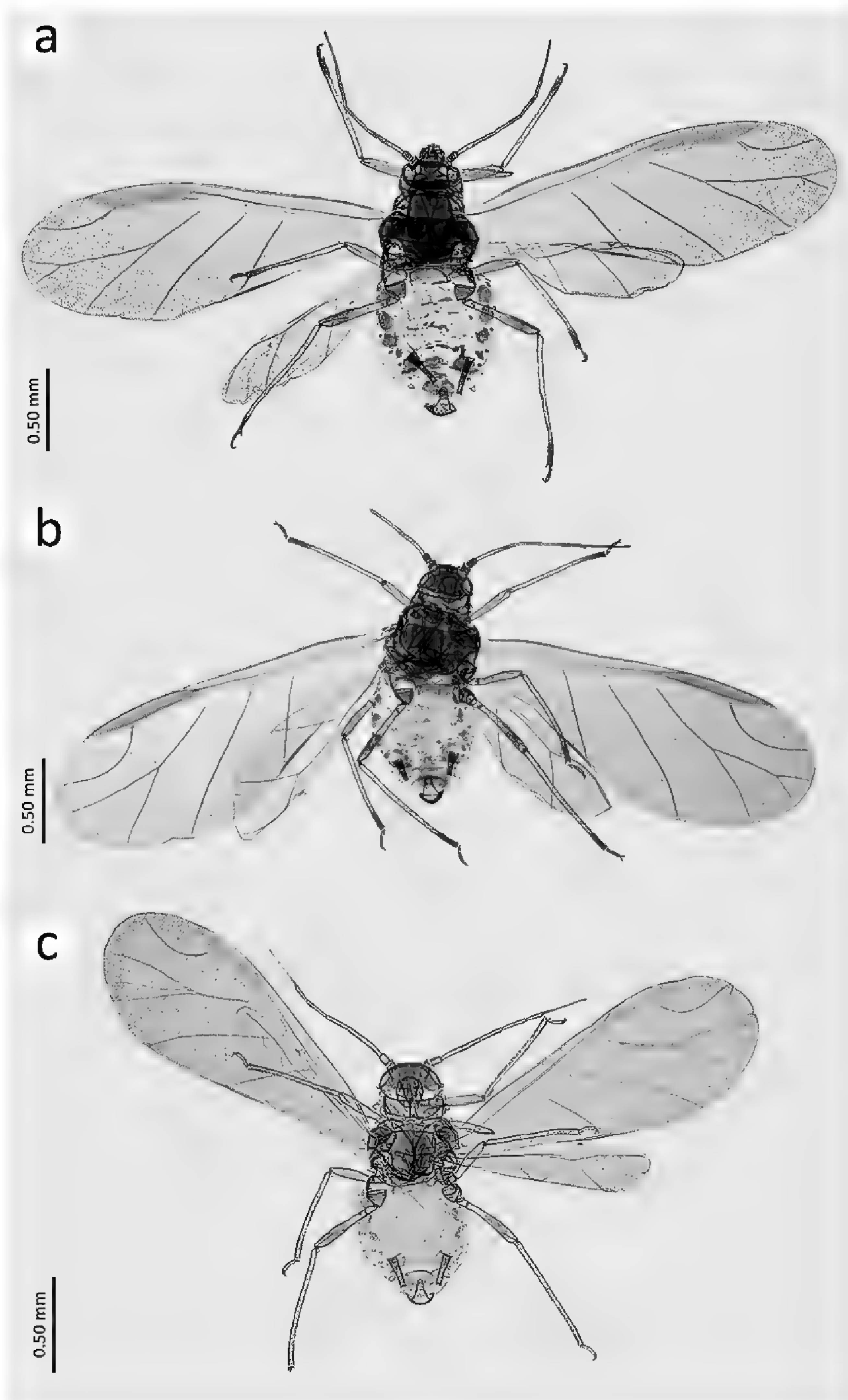
**Colour** in life: apterae are pale yellow, yellowish green, green or dark green, depending on location on host (Blackman & Eastop 2019); pigmentation on slide: head sclerotized, brown. Antennae light brown with lighter ANT and basal part of ANT IV or ANT III, and basal part of ANT IV and V. Legs yellow to pale brown with brown distal parts of tibiae and tarsi (sometimes only slightly visible). Abdomen yellow with brown to dark brown SIPH and light brown cauda and anal plate (Fig. 1a).

HW  $0.36\text{--}0.40 \times \text{ANT}$ . Head setae  $0.015\text{--}0.025$  mm long,  $0.75\text{--}0.90 \times \text{BD III}$ . ANT  $0.51\text{--}0.58 \times \text{BL}$ . ANT IV slightly shorter, as long as or slightly longer than ANT V. ANT VI with PT  $2.45\text{--}3.00 \times \text{BASE}$ . Other antennal ratios: VI:III  $1.28\text{--}1.52$ , V:III  $0.56\text{--}0.69$ , IV:III  $0.56\text{--}0.76$ , PT:III  $0.87\text{--}0.91$ , PT:IV  $1.42\text{--}1.71$ , PT:V  $1.55\text{--}1.80$ . ANT bearing very short and blunt setae (Fig. 5a). ANT III setae shorter than the width of the segment,  $0.010\text{--}0.015$  mm long, LS III  $0.50\text{--}0.75 \times \text{BD III}$ . ANT I with 4–5, ANT II with 3–5, ANT III with 4–9, ANT IV with 2–4, ANT V with 2–5, ANT VI with 2–3 basal setae. Rostrum reaching hind coxae. URS  $0.37\text{--}0.50 \times \text{ANT III}$ ,  $0.27\text{--}0.34 \times \text{ANT VI}$ ,  $0.37\text{--}0.46 \times \text{PT}$ ,  $1.09\text{--}1.37 \times \text{BASE}$  and  $1.00\text{--}1.22 \times \text{HT II}$ . Mesosternal furca wide, fused basally. III FEMORA bearing long, slightly rigid setae with blunt or slightly expanded apices (Fig. 5b),  $0.015\text{--}0.032$  mm long, III FEMORA LS  $0.63\text{--}0.76 \times$



**Fig. 1.** *Apterous viviparous* females of *Knautia* feeding *Aphis* species. (a) *A. confusa*; (b) *A. holmani* sp. nov.; (c) *A. longini*; (d) *A. thomasi*.



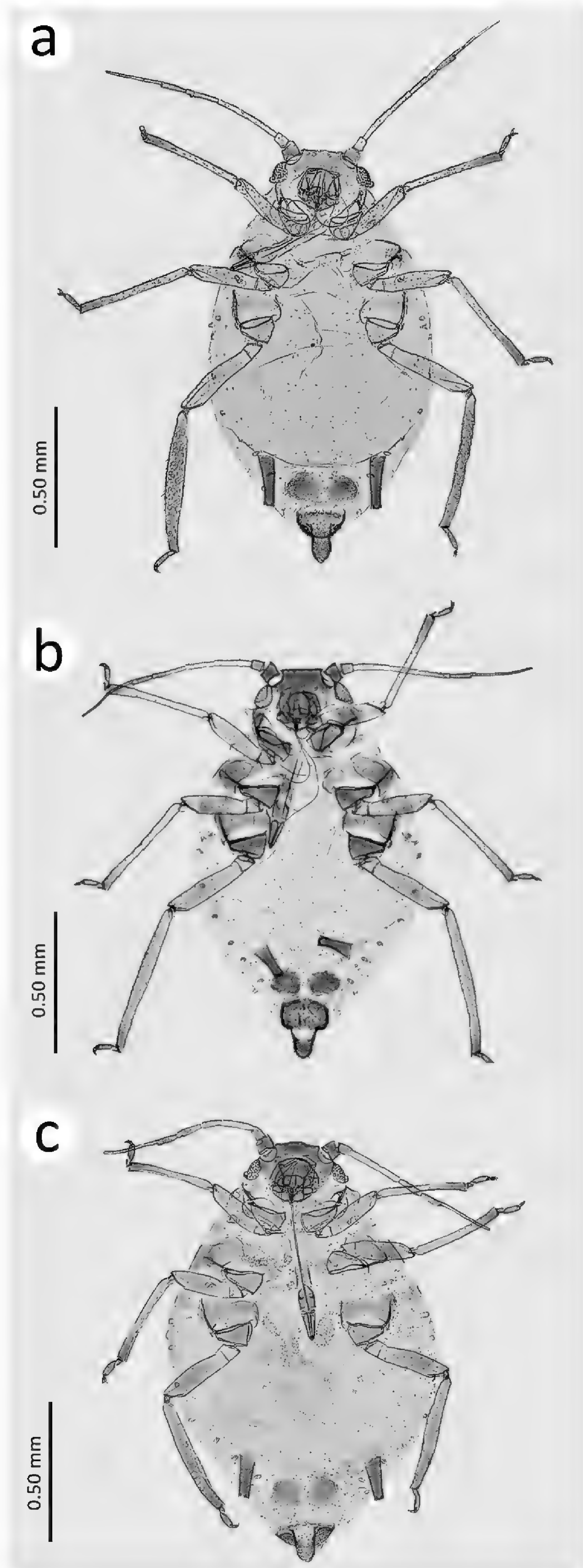


**Fig. 2.** Known alate viviparous females of *Knautia* feeding *Aphis* species. **(a)** *A. confusa*; **(b)** *A. holmani* sp. nov.; **(c)** *A. thomasi*.

trochantero-femoral suture length. Posterior seta on hind trochanter  $0.76\text{--}1.00 \times$  trochantero-femoral suture length (Fig. 5c). III TIBIAE bearing long and rigid setae with slightly blunt apices,  $0.017\text{--}0.030$  mm long. HT II  $0.37\text{--}0.44 \times$  ANT III,  $0.27\text{--}0.30 \times$  ANT VI,  $0.37\text{--}0.42 \times$  PT and  $1.00\text{--}1.12 \times$  BASE. Abdomen with very small MTu on ABD IV. SIPH  $1.60\text{--}1.88 \times$  cauda,  $0.13\text{--}0.18 \times$  BL, and  $1.09\text{--}1.30 \times$  ANT III. Setae on ABD I–V  $0.015\text{--}0.020$  mm long, about  $0.85 \times$  BD III. Setae on ABD VI–VIII  $0.017\text{--}0.025$  mm long,  $0.85\text{--}1.13 \times$  BD III. Genital plate anterior setae  $0.035\text{--}0.042$  mm long,  $1.75\text{--}2.00 \times$  BD III. Cauda with 5–8 setae (Fig. 6a, b).

*Alate viviparous female* (n=4).

**Colour** in life: unknown; pigmentation on slide: head and thorax sclerotized, brown to dark brown. Antennae brown to light brown with paler basal half of ANT III, IV and V. Wings light brown with darker venation. Fore



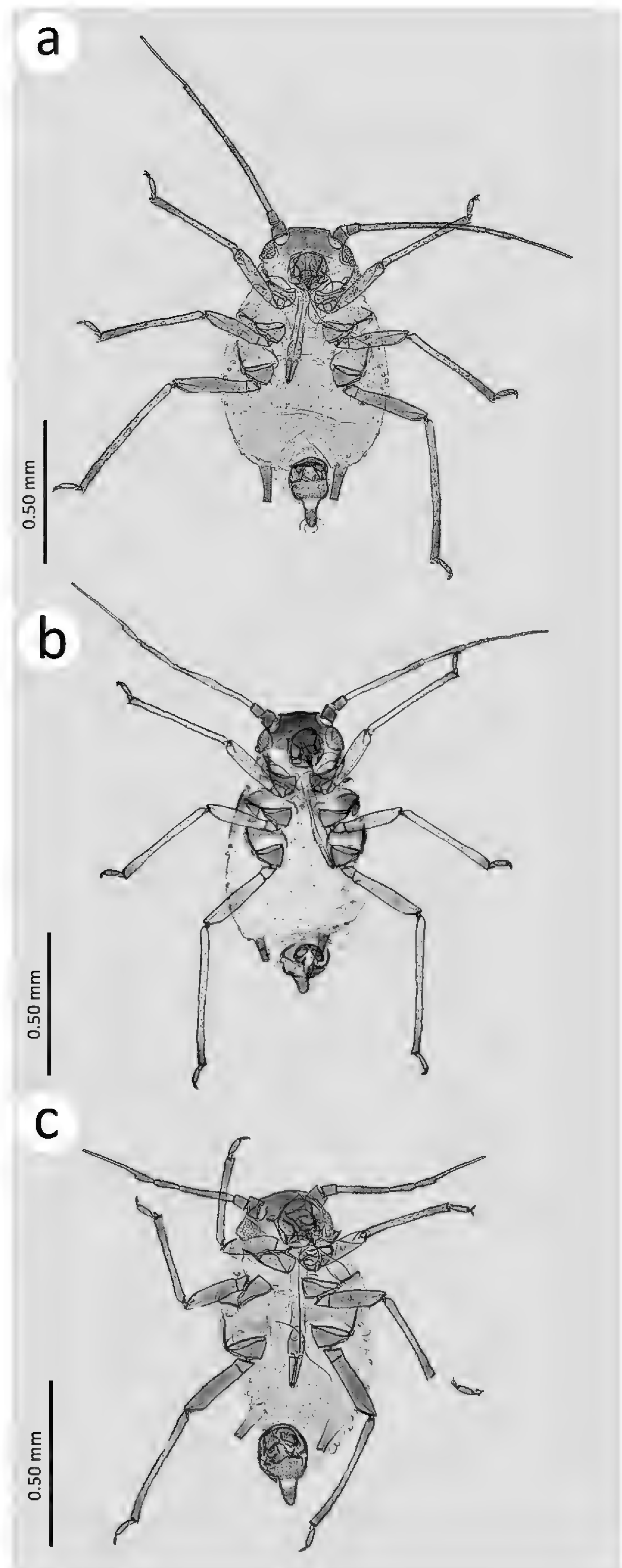
**Fig. 3.** Known oviparous females of *Knautia* feeding *Aphis* species. **(a)** *A. confusa*; **(b)** *A. holmani* sp. nov.; **(c)** *A. thomasi*.



and middle femora uniformly yellow to light brown, hind femora yellow to light brown with darker distal half. Tibiae yellow to light brown with brown distal ends and tarsi. Abdomen pale with brown sclerite, plates, SIPH, cauda and anal plate (Fig. 2a). HW  $0.34\text{--}0.36 \times \text{ANT}$ . Head setae  $0.012\text{--}0.015$  mm long,  $0.76\text{--}0.88 \times \text{BD III}$ . ANT  $0.62\text{--}0.67 \times \text{BL}$ . ANT III with 4–5 secondary rhinaria, ANT IV slightly shorter or slightly longer than ANT V. ANT VI with PT  $2.28\text{--}2.90 \times \text{BASE}$ . Other antennal ratios: VI:III  $1.32\text{--}1.70$ , V:III  $0.57\text{--}0.77$ , IV:III  $0.62\text{--}0.69$ , PT:III  $0.92\text{--}1.20$ , PT:IV  $1.33\text{--}1.93$ , PT:V  $1.55\text{--}1.70$ . ANT bearing very short and blunt setae. ANT III setae shorter than the width of the segment,  $0.010\text{--}0.012$  mm long, LS III  $0.58\text{--}0.83 \times \text{BD III}$ . ANT I with 4–5, ANT II with 4–5, ANT III with 5–7, ANT IV with 4–6, ANT V with 4–6, ANT VI with 2–3 basal setae. Rostrum reaching mesosternum. URS  $0.42\text{--}0.45 \times \text{ANT III}$ ,  $0.26\text{--}0.31 \times \text{ANT VI}$ ,  $0.37\text{--}0.45 \times \text{PT}$ ,  $0.90\text{--}1.10 \times \text{BASE}$  and  $1.10\text{--}1.17 \times \text{HT II}$ . III FEMORA bearing medium sized to long, slightly rigid setae with blunt apices,  $0.017\text{--}0.027$  mm long, III FEMORA LS  $0.59\text{--}0.67 \times \text{trochantero-femoral suture length}$ . Posterior seta on hind trochanter  $0.40\text{--}0.81 \times \text{trochantero-femoral suture length}$ . III TIBIAE bearing long and rigid setae with blunt apices,  $0.017\text{--}0.027$  mm long. HT II  $0.38\text{--}0.39 \times \text{ANT III}$ ,  $0.22\text{--}0.28 \times \text{ANT VI}$ ,  $0.32\text{--}0.41 \times \text{PT}$  and  $0.77\text{--}0.95 \times \text{BASE}$ . Abdomen with solid sclerotic bar on ABD I, small spinal and spinopleural sclerites on ABD ABD II–V. ABD V without presiphuncular sclerites. ABD VI with large spinal plate. ABD VII with small spinal plate (Fig. 7a). SIPH  $1.50\text{--}1.61 \times \text{cauda}$ , about  $0.13 \times \text{BL}$ , and  $0.87\text{--}0.95 \times \text{ANT III}$ . Setae on ABD I–V  $0.010\text{--}0.015$  mm long,  $0.66\text{--}0.88 \times \text{BD III}$ . Setae on ABD VI–VIII  $0.015\text{--}0.020$  mm long,  $0.88\text{--}1.17 \times \text{BD III}$ . Genital plate anterior setae  $0.020\text{--}0.040$  mm long,  $1.47\text{--}2.35 \times \text{BD III}$ . Cauda with 5–7 setae.

*Oviparous female* (n=4).

*Colour* in life: unknown; pigmentation on slide: head slightly sclerotized, yellow to light brown. Antennae yellow or pale with ANT I, ANT II, apical part of ANT V, BASE and PT light brown. Legs yellow with light brown distal parts of tibiae and tarsi. Hind tibiae uniformly light brown. Abdomen yellow with brown SIPH, cauda and anal plate (Fig. 3a). HW  $0.47\text{--}0.50 \times \text{ANT}$ . Head setae  $0.010\text{--}0.012$  mm long,  $0.58\text{--}0.62 \times \text{BD III}$ . ANT about  $0.48 \times \text{BL}$ . ANT IV slightly shorter than ANT V. ANT VI with PT about  $2.50 \times \text{BASE}$ . Other antennal ratios: VI:III  $2.00\text{--}2.33$ , V:III  $0.85\text{--}0.91$ , IV:III  $0.64\text{--}0.83$ , PT:III  $1.42\text{--}1.66$ , PT:IV  $2.20\text{--}2.22$ , PT:V  $1.66\text{--}1.81$ . ANT bearing very short and blunt setae. ANT III setae shorter than the width of the segment,  $0.007\text{--}0.010$  mm long, LS III  $0.58\text{--}0.62 \times \text{BD III}$ . ANT I with 5, ANT II with 3, ANT III with 5–6, ANT IV with 2, ANT V with 3–4, ANT VI with 2–3 basal setae. Rostrum reaching hind coxae. URS  $0.67\text{--}0.83 \times \text{ANT III}$ ,  $0.33\text{--}0.35 \times \text{ANT VI}$ ,  $0.47\text{--}0.50 \times \text{PT}$ ,  $1.18\text{--}1.25 \times \text{BASE}$  and  $1.18\text{--}1.33$



**Fig. 4.** Known males of *Knautia* feeding *Aphis* species. (a) *A. confusa*; (b) *A. holmani* sp. nov.; (c) *A. thomasi*.



**Table 1.** Morphological differences between apterous and alate viviparous females of *Aphis holmani* sp. nov. and *A. confusa*.

Character	Apterous viviparous females	
	<i>Aphis holmani</i> sp. nov.	<i>Aphis confusa</i>
Femora setae	pointed	with blunt apices
Head setae	pointed	with blunt apices
URS	0.13–0.16	0.10–0.12
III FEMUR LS	0.045–0.050	0.030–0.045
Head LS	0.030–0.035	0.015–0.025
Frontal setae	0.030–0.035	0.017–0.025
ABD VIII setae	0.025–0.030	0.017–0.025
GP anterior setae L	0.045–0.050	0.035–0.042
PT/BASE	1.75–2.20	2.45–3.00
URS/HT II	1.40–1.52	1.00–1.22
URS/ANT VI	0.40–0.43	0.27–0.34
URS/PT	0.59–0.66	0.37–0.45
HT II/ANT III	0.26–0.35	0.37–0.44
HT II/BASE	0.83–0.90	1.00–1.25
SIPH/CAUDA	1.05–1.50	1.60–1.88
SIPH/ANT III	0.59–0.91	1.09–1.30
III FEMUR LS/TFS	0.90–1.11	0.63–0.76
GP anterior seta/ BD III	2.25–2.94	1.75–2.00
ABD VIII setae/BD III	1.11–1.76	0.85–0.90

	Alate viviparous females	
	<i>Aphis holmani</i> sp. nov.	<i>Aphis confusa</i>
URS	0.125–0.135	0.100–0.110
III FEMUR LS	0.032–0.035	0.022–0.025
ABD I–V setae	0.020–0.025	0.010–0.015
ABD VI–VIII setae	0.025–0.040	0.015–0.020
HW/ANT	0.32–0.33	0.34–0.36
URS/HT II	1.50–1.56	1.10–1.17
URS/ANT III	0.51–0.59	0.42–0.45
URS/ANT VI	0.36–0.37	0.26–0.31
URS/PT	0.51–0.52	0.37–0.45
URS/BASE	1.25–1.28	0.90–1.10
SIPH/CAUDA	1.14–1.36	1.50–1.61
SIPH/BL	0.090–0.010	0.13
SIPH/ANT III	0.57–0.58	0.87–0.95
III FEMU LS/TFS	0.80–0.86	0.59–0.67
Head setae/BD III	0.11–0.14	0.08–0.09
Frontal setae/BD III	0.13–0.16	0.07–0.10
ABD I–V setae/BD III	0.13	0.006–0.008
ABD VI–VIII setae/BD III	0.16	0.08–0.11

× HT II. Mesosternal furca separated or slightly fused, wide. Posterior seta on hind trochanter 0.64–1.00 × trochantero-femoral suture length. III FEMORA with 60–89 pseudosensoria, bearing medium sized to long, slightly rigid setae with slightly blunt apices which are mostly pointed on the dorsal side, 0.010–0.075 mm long, III FEMORA LS 0.59–0.77 × trochantero-femoral suture length. III TIBIAE with 60–89 mostly circular, different in size pseudosensoria and with long and rigid setae with blunt apices, 0.010–0.030 mm long. HT II 0.57–0.62 × ANT III, 0.26–0.28 × ANT VI, 0.37–0.40 × PT and 0.93–

1.00 × BASE. Abdomen with small marginal tubercles on ABD I, V and VII. SIPH 1.23–1.28 × cauda, about 0.11 × BL, and 1.28–1.33 × ANT III. Setae on ABD I–V 0.010–0.015 mm long, about 0.62–0.88 × BD III. Setae on ABD VI–VIII 0.015–0.025 mm long, 0.93–1.00 × BD III. Genital plate anterior setae 0.026–0.035 mm long, 1.52–2.18 × BD III. Cauda with 6–7 setae.

*Male* (n=5).  
*Colour* in life: unknown; pigmentation on slide: head sclerotized, light brown. Antennae light brown with



**Table 2.** Morphological differences between sexual morphs of *Aphis holmani* sp. nov. and *A. confusa*.

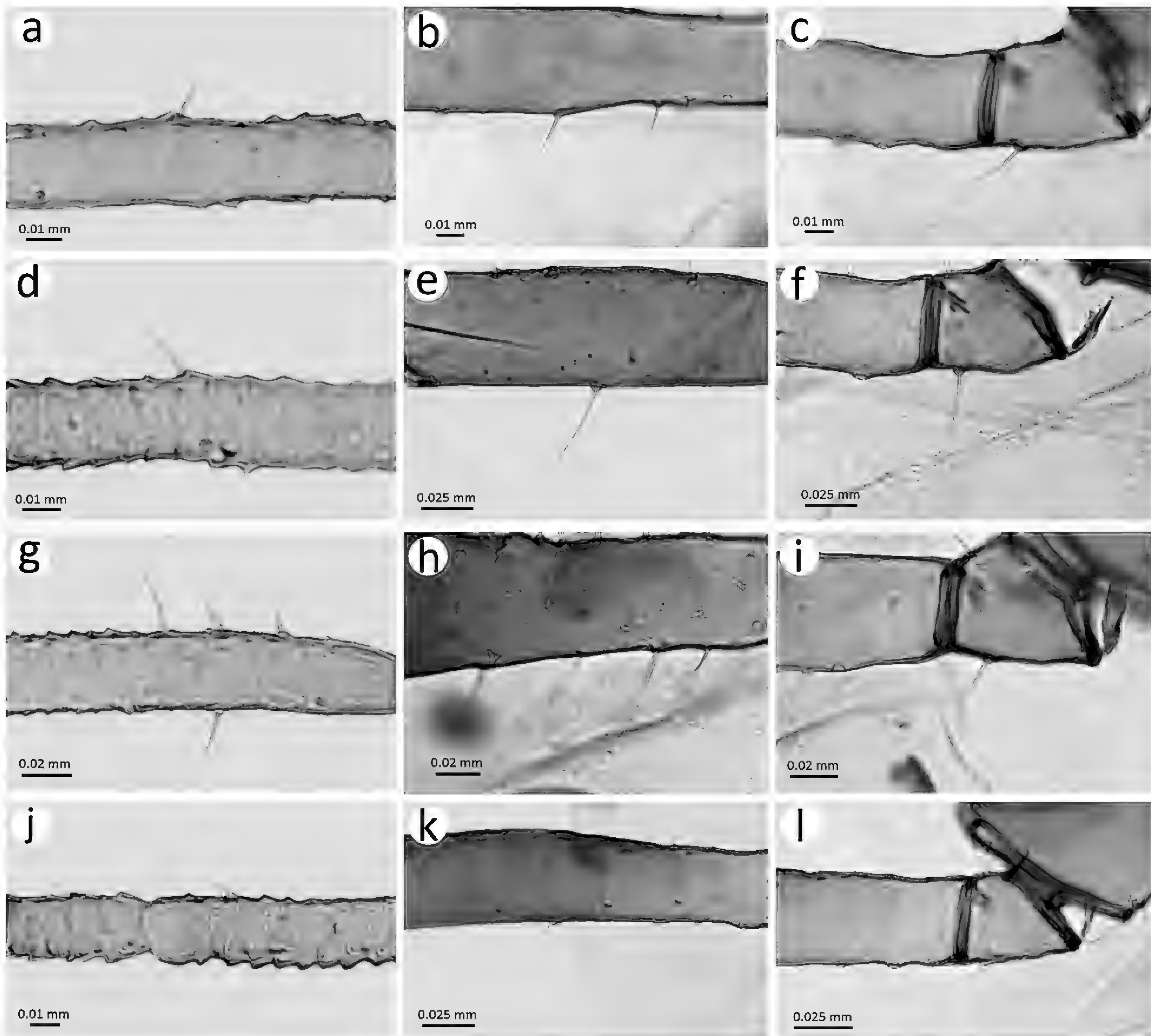
Character	Oviparous females	
	<i>Aphis holmani</i> sp.nov.	<i>Aphis confusa</i>
Tibiae setae	pointed	with blunt apices
Pseudosensoria	25–42	60–89
ABD VIII setae	8–10	3–5
ANT	0.77–0.85	0.70–0.73
III FEMUR LS	0.04–0.05	0.025–0.035
TIBIAE LS	0.035–0.045	0.01–0.03
Head setae	0.017–0.040	0.010–0.012
Frontal setae	0.030–0.040	0.015–0.025
ABD I–V setae	0.032–0.075	0.010–0.015
ABD VIII setae	0.025–0.030	0.015–0.025
ANT/BL	0.51–0.56	0.48
HW/ANT	0.44–0.46	0.47–0.50
PT/BASE	2.68–3.06	2.50
URS/BASE	1.37–1.43	1.18–1.25
SIPH/CAUDA	1.07–1.12	1.23–1.28
SIPH/BL	0.08–0.09	0.11
SIPH/ANT III	0.87–0.96	1.28–1.33
III FEMUR LS/TFS	0.84–1.00	0.57–0.77
GP anterior seta/ BD III	2.50–3.23	1.52–2.18
Head setae/BD III	0.85–1.47	0.58–0.62
ABD I–V setae/BD III	1.10–1.29	0.62–0.88
ABD VI–VIII setae/BD III	1.88–2.00	0.93–1.00

	Males	
	<i>Aphis holmani</i> sp. nov.	<i>Aphis confusa</i>
ANT IV rhinaria	12–18	2–12
ANT V rhinaria	11–13	4–10
TFS	0.032–0.037	0.040–0.045
ABD I–V setae	0.022–0.027	0.010–0.013
ABD VI–VIII setae	0.030–0.052	0.015–0.030
ANT/BL	0.87–1.06	0.76–0.80
HW/ANT	0.31–0.36	0.39–0.40
PT/BASE	2.94–3.28	2.64–2.73
ANT V/ANT III	0.82–0.83	0.76–0.80
ANT IV/ANT III	0.82–0.88	0.61–0.71
ANT IV/ANT V	1.00–1.06	0.80–0.89
URS/HT II	1.33–1.35	1.21–1.30
URS/ANT III	0.55	0.48–0.50
HT II/BASE	0.88–1.00	0.82–0.86
SIPH/CAUDA	0.88–0.90	1.00–1.20
SIPH/ANT III	0.47–0.50	0.57–0.64
III FEMUR LS/TFS	1.06–1.08	0.78–0.80
Head setae/BD III	1.11–1.33	0.50–0.76
Frontal setae/BD III	1.33	0.60–0.96
ABD I–V setae/BD III	1.46–1.80	0.50–0.076
ABD VI–VIII setae/BD III	2.00–2.46	0.75–1.15

slightly paler basal part of ANT III. Legs with yellow or light brown femora and pale to yellow tibiae with brown distal parts and tarsi. Abdomen pale with light brown SIPH, cauda and genitalia (Fig. 4a). HW 0.39–0.40 ×

ANT. Head setae 0.010–0.017 mm long, 0.50–0.76 × BD III. ANT 0.76–0.80 × BL. ANT III with 0 (on one segment)–14, ANT IV shorter, than ANT V with 2–12, ANT V with 1–11 secondary rhinaria. ANT VI with PT





**Fig. 5.** Key morphological differences between apterous viviparous females of *Knautia* feeding *Aphis* species. *A. confusa*: (a) ANT III seta with blunt apex; (b) hind femora inner setae with blunt apices; (c) long hind trochanter seta; *A. holmani* sp. nov.: (d) ANT III seta with pointed apex; (e) hind femora inner setae with pointed apices; (f) very long hind trochanter seta; *A. longini*: (g) ANT III long and pointed setae; (h) hind femora inner setae with pointed apices; (i) long hind trochanter seta; *A. thomasi*: (j) ANT III and IV very short setae with blunt apices; (k) very short hind trochanter inner setae with blunt apices; (l) very short hind trochanter seta.

2.64–2.73 × BASE. Other antennal ratios: VI:III 1.64–1.77, V:III 0.76–0.80, IV:III 0.61–0.71, PT:III 1.20–1.28, PT:IV 1.80–1.95, PT:V 1.57–1.60. ANT bearing very short and blunt setae. ANT III setae shorter than the width of the segment, about 0.010 mm long, LS III 0.50–0.76 × BD III. ANT I with 4–5, ANT II with 3, ANT III with 4–5, ANT IV with 3, ANT V with 1–3, ANT VI with 1–2 basal setae. Rostrum reaching from hind coxae to ABD I. URS 0.48–0.50 × ANT III, 0.27–0.30 × ANT VI, 0.37–0.41 × PT, 1.00–1.33 × BASE and 1.21–1.30 × HT II. Mesosternal furca separated. Posterior seta on hind trochanter 1.00–1.40 × trochantero-femoral suture

length. III FEMORA bearing short to medium sized and rigid setae with mostly blunt apices which are pointed on the dorsal side, 0.015–0.032 mm long, III FEMORA LS 0.78–0.80 × trochantero-femoral suture length. III TIBIAE bearing short to medium sized and rigid setae with blunt apices, 0.010–0.025 mm long. HT II 0.38–0.40 × ANT III, 0.22–0.23 × ANT VI, about 0.31 × PT and 0.82–0.86 × BASE. Abdomen with small marginal tubercles on ABD IV. SIPH 1.00–1.22 × cauda, 0.09–0.11 × BL, and 0.57–0.64 × ANT III. Setae on ABD I–V 0.010–0.013 mm long, 0.50–0.76 × BD III. Setae on ABD VI–



VIII 0.015–0.030 mm long,  $0.75\text{--}1.15 \times \text{BD III}$ . Cauda with 4–6 setae.

**Material examined.** CZECH REPUBLIC: Český Krumlov-Vyšné, 27 May 1987, on *Knautia arvensis*, J. Holman leg., 2 al, 19705, IECA; Karlštejn, 10 October 1971, on *K. arvensis*, J. Holman leg., 4 ♀, 5 ♂, 13289, IECA; FRANCE: Nevache (1600m), dépt. Hautes-Alpes, 25 June 1969, on *K. arvensis*, F. Leclant leg., 2 apt, L3120, IECA; HUNGARY: Nagykovácsi: Nagyszénás, 17 June 1964, on *Scabiosa* sp., H. Szelegiewicz leg., 6 apt, 2225, R344, ZMPA; on *S. ochroleuca*, H. Szelegiewicz leg., 6 apt, 2782, R434, ZMPA; POLAND: Ługwałd near Olsztyn, 27 June 1964, on *K. arvensis*, S. Huculak leg., 3 apt (per one on each slide), 189, R341, ZMPA; Kaletnik near Suwałki, 09 July 1955, on *K. arvensis*, H. Szelegiewicz leg., 4 apt, 32 R348, 1 al, 32 R439, ZMPA; SLOVAKIA: Vrbovce, 20 May 1967, on *K. arvensis*, J. Holman leg., 4 apt, 10879 (apt. 33–36), IECA; SWEDEN: Växjö, S. Åreda, 06 June 1981, R. Danielsson leg., 2 apt, 1 al, 5132: 24, IECA.

**Host plants.** *Dipsacus* sp. *D. fullonum*, *Knautia arvensis*, *K. integrifolia*, *K. dinarica*, *K. dipsacifolia*, *K. longifolia*, *Scabiosa* sp., *S. argentea*, *S. atropurpurea*, *S. canescens*, *S. columbaria*, *S. comosa*, *S. ochroleuca*, *S. sosnowskyi*, *S. pratensis* (Holman 2009)

**Biology.** This is a monoecious and holocyclic species with sexuales in September and October. The aphids occur on upper parts of stems and inflorescences or on undersides of leaves and at base of stems or on roots (Heie 1986).

**Distribution.** *Aphis confusa* is a common and widely distributed species in Europe (except Balkans).

#### *Aphis (Aphis) holmani* sp. nov.

*Aphis knautiae* Holman in Holman & Pintera, 1981: 50 (nomen nudum)

Figs 1–7, Supplementary tables 1–4; Tables 1–2

#### Description

##### *Apterous viviparous female* (n=63).

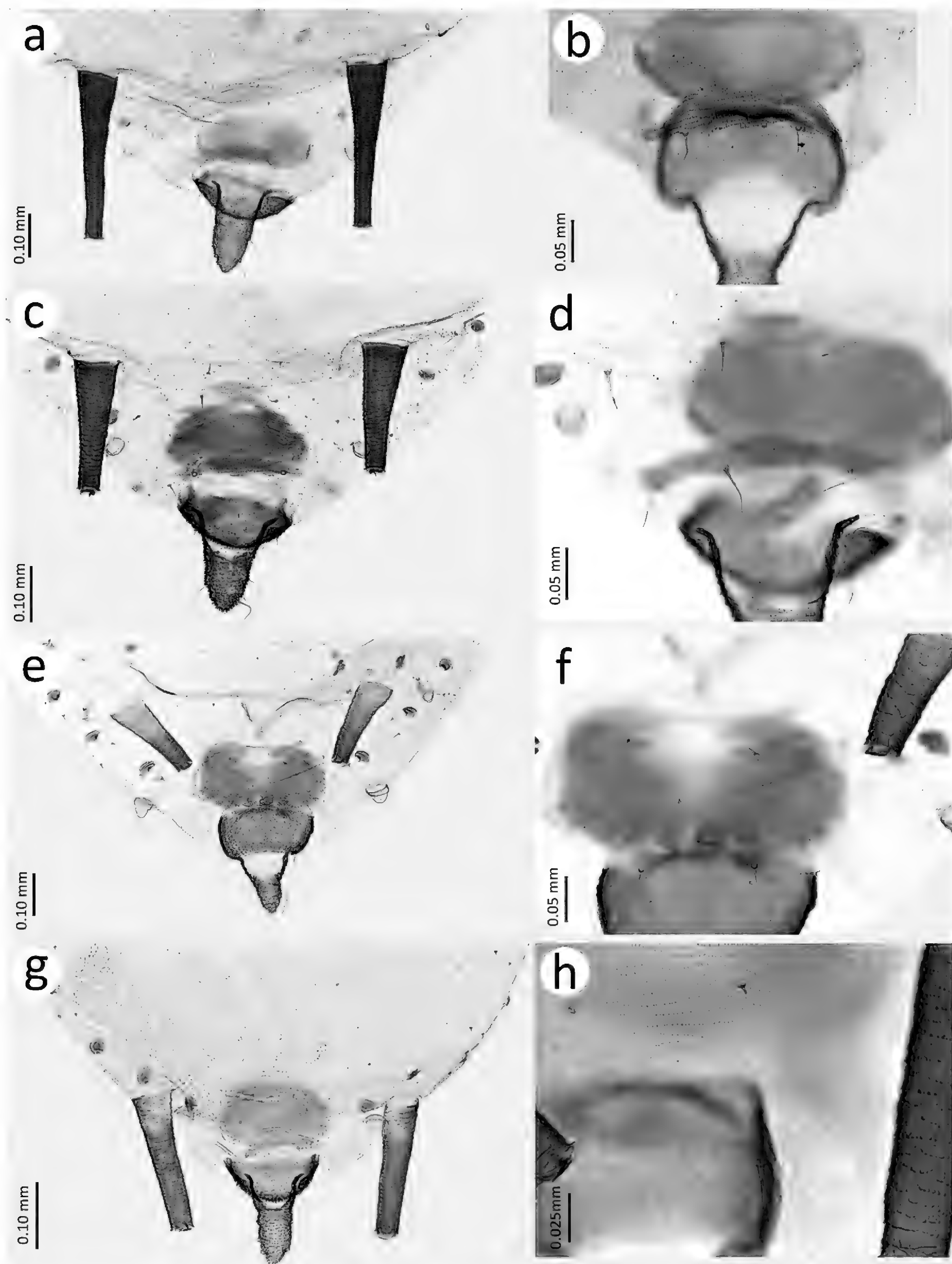
**Colour** in life: unknown; pigmentation on slide: head slightly sclerotized, light brown. Antennae yellow or light yellow with ANT I and ANT II and light brown, apical part of ANT V and BASE and PT pale brown. Legs yellow with light brown distal parts of tibiae and tarsi. Abdomen yellow with light brown to brown SIPH, cauda and anal plate (Fig. 1b). HW  $0.36\text{--}0.45 \times \text{ANT}$ . Head setae 0.015–0.035 mm long,  $0.83\text{--}1.25 \times \text{BD III}$ . ANT  $0.46\text{--}0.52 \times \text{BL}$  in 5-segmented specimens and  $0.60\text{--}0.62 \times \text{BL}$  in 6-segmented specimens. In 6-segmented speci-

mens ANT IV slightly shorter or as long as ANT V. ANT VI with PT  $1.75\text{--}2.20 \times \text{BASE}$ . Other antennal ratios: VI:III 0.86–1.33, V:III 0.45–0.62, IV:III 0.54–0.57 (in 6-segmented specimens), PT:III 0.55–0.91, PT:IV 1.26–1.69, PT:V 1.16–1.57. ANT bearing very short and pointed setae (Fig. 5d). ANT III setae shorter than the width of the segment, 0.010–0.125 mm long, LS III  $0.50\text{--}1.00 \times \text{BD III}$ . ANT I with 4–6, ANT II with 3–5, ANT III with 5–11, ANT IV with 3–5, ANT V with 2–4, ANT VI with 1–2 basal and 4 apical setae. Rostrum reaching from hind coxae to ABD I. URS  $0.36\text{--}0.54 \times \text{ANT III}$ ,  $0.40\text{--}0.43 \times \text{ANT VI}$ ,  $0.59\text{--}0.66 \times \text{PT}$ ,  $1.16\text{--}1.30 \times \text{BASE}$  and  $1.40\text{--}1.52 \times \text{HT II}$  with 2–4 accessory setae. Mesosternal furca separated or slightly fused, wide. III FEMORA bearing long, fine, hair-like setae with pointed apices (Fig. 5e), 0.015–0.050 mm long, III FEMORA LS  $0.045\text{--}0.050$  mm long,  $0.90\text{--}1.11 \times \text{trochantero-femoral suture length}$ . Posterior seta on hind trochanter,  $1.00\text{--}1.22 \times \text{trochantero-femoral suture length}$  (Fig. 5f). III TIBIAE bearing long setae with pointed apices, 0.010–0.040 mm long. HT I with 3–3–2 ventral setae, HT II  $0.26\text{--}0.35 \times \text{ANT III}$ ,  $0.26\text{--}0.30 \times \text{ANT VI}$ ,  $0.38\text{--}0.47 \times \text{PT}$  and  $0.83\text{--}0.90 \times \text{BASE}$ . Abdomen membranous, with well-developed marginal tubercles on ABD I and ABD VII and sometimes small marginal tubercles on ABD IV. SIPH tubular, very slightly tapering towards apex,  $1.05\text{--}1.50 \times \text{cauda}$ ,  $0.09\text{--}0.14 \times \text{BL}$ , and  $0.59\text{--}0.91 \times \text{ANT III}$ . Dorsal setae very short and pointed, 0.015–0.030 mm long,  $0.83\text{--}1.25 \times \text{BD III}$  on ABD I–V and 0.020–0.055 mm long,  $1.11\text{--}1.76 \times \text{BD III}$  on ABD VI–VIII. Anterior setae on genital plate 0.045–0.050 mm long,  $2.25\text{--}2.94 \times \text{BD III}$ . Cauda with 6–9 setae (Fig. 6c, d).

##### *Alate viviparous female* (n=5).

**Colour** in life: unknown; pigmentation on slide: head and thorax sclerotized, brown. ANT light brown with brown ANT I and ANT II and slightly paler basal half of ANT III–V. Fore and middle legs light brown with slightly darker distal parts of tibiae. Hind legs with brown femora with paler proximal parts and light brown tibiae with darker distal part of tibiae and tarsi. Wings with light brown pterostigma and veins. Abdomen pale with light brown sclerotization, brown SIPH and cauda (Fig. 2b). HW about  $0.32 \times \text{ANT}$ . Head setae 0.017–0.027 mm long,  $0.11\text{--}0.14 \times \text{BD III}$ . ANT  $0.65\text{--}0.76 \times \text{BL}$ . ANT III with 4–6 secondary rhinaria. ANT IV as long as or slightly shorter, as long as than ANT V with 0–1 secondary rhinaria. ANT VI with PT  $2.40\text{--}2.47 \times \text{BASE}$ . Other antennal ratios: VI:III 1.40–1.61, V:III 0.57–0.66, IV:III 0.51–0.61, PT:III 1.00–1.14, PT:IV 1.73–1.84, PT:V 1.71–1.73. ANT bearing very short and blunt setae. ANT III setae shorter than the width of the segment, 0.012–0.015 mm long, LS III  $0.80\text{--}1.00 \times \text{BD III}$ . ANT I with 4–5, ANT II with 3–5, ANT III with 6–10, ANT IV with 3–6, ANT V with 4–6, ANT VI with 2 basal setae. Rostrum reaching from hind coxae to ABD I. URS  $0.51\text{--}$





**Fig. 6.** End of abdomen (left column) and ABD VIII setae (right column) of *Knautia* feeding *Aphis* species. (a–b) *A. confusa*, (c–d) *A. holmani* sp. nov., (e–f) *A. longini*, (g–h) *A. thomasi*.



0.59 × ANT III, about 0.36 × ANT VI, 0.51–0.52 × PT, 1.25–1.28 × BASE and 1.50–1.56 × HT II. III FEMORA bearing long, fine and pointed setae, 0.012–0.032 mm long, III FEMORA LS 0.80–0.86 × trochantero-femoral suture length. Posterior seta on hind trochanter 0.80–1.00 × trochantero-femoral suture length. III TIBIAE bearing long, fine and pointed setae, 0.012–0.032 mm long. HT II 0.34–0.38 × ANT III, 0.23–0.26 × ANT VI, 0.33–0.34 × PT and 0.80–1.00 × BASE. Abdomen with sclerite on ABD I, small spinal sclerites on ABD II–IV. ABD V with solid or broken presiphuncular sclerites. ABD VI with large spinal plate. ABD VII with wide spino-pleural plate. ABD IV and VI with small MTu (Fig. 7b). SIPH 1.14–1.636 × cauda, 0.09–0.10 × BL, and about 0.57 × ANT III. Setae on ABD I–V 0.020–0.025 mm long, about 1.33 × BD III. Setae on ABD VI–VIII 0.025–0.040 mm long, about 1.66 × BD III. Genital plate anterior setae 0.030–0.040 mm long, 2.00–2.66 × BD III. Cauda with 8 setae.

*Oviparous female* (n=47).

*Colour* in life: unknown; pigmentation on slide: head sclerotized, brown. Antennae pale with ANT I, ANT II, apical part of ANT V and ANT VI brown. Legs yellow with slightly darker very apical parts and tarsi. Abdomen yellow with brown SIPH, cauda and anal plate (Fig. 3b). HW 0.44–0.46 × ANT. Head setae 0.017–0.040 mm long, 0.85–1.47 × BD III. ANT 0.51–0.56 × BL. ANT IV shorter than ANT V. ANT VI with PT 2.68–3.06 × BASE. Other antennal ratios: VI:III 2.00–2.18, V:III 0.87–0.92, IV:III 0.70–0.85, PT:III 1.48–1.51, PT:IV 1.86–2.09, PT:V 1.64–1.75. ANT bearing very short and pointed setae. ANT III setae shorter than the width of the segment, 0.011–0.015 mm long, LS III 0.60–0.88 × BD III. ANT I with 4–5, ANT II with 4, ANT III with 3–4, ANT IV with 2–3, ANT V with 2–3, ANT VI with 2–3 basal setae. Rostrum reaching hind coxae. URS 0.70–0.81 × ANT III, 0.35–0.37 × ANT VI, 0.35–0.37 × PT, 1.37–1.43 × BASE and 1.22–1.43 × HT II. Mesosternal furca fused and wide. III FEMORA with 25–42 pseudosensoria, bearing long, fine and pointed setae, 0.015–0.050 mm long, III FEMORA LS 0.84–1.00 × trochantero-femoral suture length. Posterior seta on hind trochanter 0.74–1.11 × trochantero-femoral suture length. III TIBIAE bearing long, fine and pointed setae, 0.017–0.045 mm long. HT II 0.50–0.62 × ANT III, 0.24–0.29 × ANT VI, 0.32–0.39 × PT and 1.00–1.12 × BASE. SIPH 1.07–1.12 × cauda, 0.08–0.09 × BL, and 0.87–0.96 × ANT III. Setae on ABD I–V 0.022–0.027 mm long, 1.10–1.29 × BD III. Setae on ABD VI–VIII 0.032–0.075 mm long, 1.88–2.00 × BD III. Genital plate anterior setae 0.050–0.055 mm long, 2.50–3.23 × BD III. Cauda with 6–10 setae.

*Male* (n=16).

*Colour* in life: unknown; pigmentation on slide: head slightly sclerotized, brown. Antennae light brown to

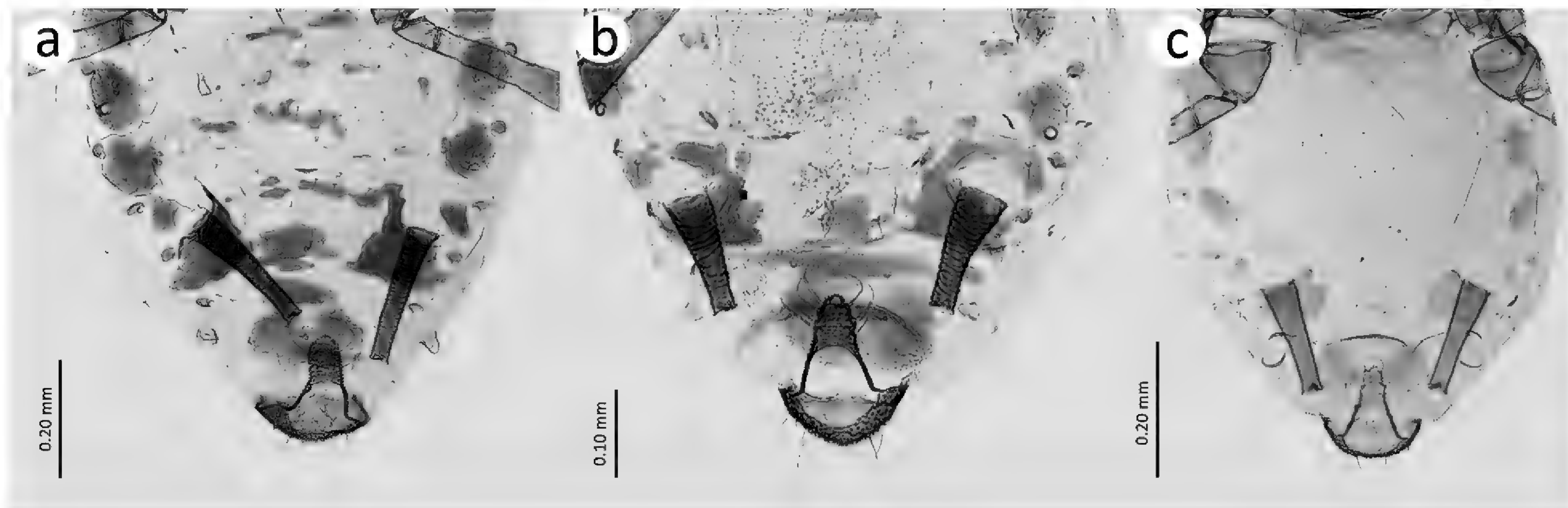
brown with yellow ANT III, basal part of ANT IV and ANT V. Legs yellow with light brown very distal parts of tibiae and tarsi. Abdomen pale with light brown to brown SIPH, cauda and anal plate (Fig. 4b). HW 0.31–0.36 × ANT. Head setae 0.017–0.025 mm long, 1.11–1.33 × BD III. ANT 0.87–1.06 × BL. ANT III with 10–16 secondary rhinaria. ANT IV as long as or slightly longer than ANT V with 12–18 secondary rhinaria. ANT V with 11–13 secondary rhinaria. ANT VI with PT 2.94–3.28 × BASE. Other antennal ratios: VI:III 1.76–1.86, V:III 0.82–0.83, IV:III 0.82–0.88, PT:III 1.35–1.38, PT:IV 1.56–1.64, PT:V 1.64–1.66. ANT bearing very short and pointed setae. ANT III setae shorter than the width of the segment, 0.011–0.012 mm long, LS III about 0.83 × BD III. ANT I with 4–5, ANT II with 4, ANT III with 4–5, ANT IV with 3, ANT V with 2–3, ANT VI with 2 basal setae. Rostrum reaching from hind coxae to ABD I. URS about 0.55 × ANT III, 0.29–0.31 × ANT VI, 0.40–0.41 × PT, 1.17–1.35 × BASE and 1.33–1.35 × HT II. III FEMORA bearing long, fine and pointed setae, 0.017–0.040 mm long, III FEMORA LS 1.06–1.08 × trochantero-femoral suture length. Posterior seta on hind trochanter 1.00–1.06 × trochantero-femoral suture length. III TIBIAE bearing long, fine and pointed setae, 0.012–0.032 mm long. HT II about 0.41 × ANT III, 0.22–0.23 × ANT VI, about 0.30 × PT and 0.88–1.00 × BASE. Abdomen with small marginal tubercles on ABD VI. SIPH 0.88–0.90 × cauda, 0.08–0.10 × BL, and 0.47–0.50 × ANT III. Setae on ABD I–V 0.022–0.027 mm long, 1.46–1.80 × BD III. Setae on ABD VI–VIII 0.030–0.052 mm long, 2.00–2.46 × BD III. Cauda with 5–6 setae.

**Diagnosis**

From so far known *Aphis* species feeding on *Knautia*, apterous viviparous females of *A. holmani* sp. nov. are most similar to *A. confusa* by hind femora and hind trochanter setae lengths (which are longer than 0.50 × trochantero-femoral suture length) and genital plate anterior setae lengths (which are longer than 1.00 × BD III). Both species differ from *A. thomasi* in those characters (0.20–0.50 × trochantero-femoral suture setae length and 0.20–0.50 × BD III respectively). The new species differ from *A. confusa* by:

- Pointed setae on femora, head and antennae (setae with blunt apices in *A. confusa*)
- longer anterior setae on the genital plate, 2.25–2.94 × BD III (1.00–2.00 in *A. confusa*)
- higher ratio of URS/HT II, 1.40–1.52 (1.00–1.22 in *A. confusa*)
- lower ratio of PT/BASE, 1.75–2.20 (2.45–3.00 in *A. confusa*)
- lower ratio of SIPH/cauda, 1.05–1.50 (1.60–1.88 in *A. confusa*)





**Fig. 7.** Key morphological differences between known alate viviparous females of *Knautia* feeding *Aphis* species. **(a)** abdomen of *A. confusa* without presiphuncular sclerites; **(b)** abdomen of *A. holmani* sp. nov. with presiphuncular sclerites; **(c)** abdomen of *A. thomasi* without presiphuncular and spino-pleural sclerites.

Detailed morphological differences between particular morphs of both species are given in Tables 1 and 2.

**Etymology.** The authors have the pleasure to give the name to honour the late Jaroslav Holman (1931–2014) – an outstanding European aphidologist and a long-time employee of the Biology Centre CAS in České Budějovice, Czech Republic.

**Biology and distribution.** The new aphid species is associated with *Knautia drymeia* Heuff., from which it was collected in Central (the Czech Republic) and South-Eastern Europe (Bulgaria and Romania). It is a holocyclic aphid with the sexual phase in September.

**Material examined.** HOLOTYPE: CZECH REPUBLIC, Jihomoravský kraj, Pustý žleb, Moravský kras, 20 June 1967, on *Knautia drymeia*, J. Holman leg., 1 apt, 10838 B (apt. 8), IECA. PARATYPES: CZECH REPUBLIC, the same data as in the holotype, 11 slides (1 apt on each slide), 10838 B (apt. 1–7, 9–12); Macocha, 19 May 1967, on *K. drymeia*, J. Holman leg., 1 apt, 10877 (apt. 1), 16 apt (two on each slide), 10877 (apt. 2–17), IECA, slide no apt.2 DZUS; Pustý žleb, 22 September 1970, on *K. drymeia*, J. Holman leg., 40 ♀ (four on each slide), 12885 (♀ 21–48, ♀ 61–68) 6 ♀, 10877 (73–78); 12 ♂ (four on each slide), 12885 (♂ 1–12), 1 ♀, 4 ♂ (♂ 13–16, ♀ 49), IECA; BULGARIA, Mt. Vitoša nr. Simenovo, 22 May 1990, on *K. drymeia*, J. Holman leg., 2 apt, 21725 A (apt. 1–2), 4 apt, 21725 (apt. 3–6), 16 apt (four on each slide), 21722 B (apt. 1–16), 2 al, 21722 B (al. 1–2), 3 al, 21722 B (al. 3–5), IECA; ROMANIA, Băile Herculane jud. Caraș-Sev, 20 July 1976, on *K. drymeia*, J. Holman leg., 12 apt (six per each slide), 16309 (apt. 1–12), IECA.

*Aphis (Aphis) longini* Huculak, 1968

Huculak, 1968: 333

Figs 1, 5, 6; Supplementary table 1

*Apterous viviparous female* (n=5).

**Colour in life:** matt dirty green to olive brown (Huculak, 1968); pigmentation on slide; head sclerotized, brown. Antennae brown with yellow ANT III and basal part of ANT IV. Femora of legs brown with lighter basal parts, tibiae light brown to yellow with brown to dark brown distal and apical parts and tarsi. Abdomen yellow to light brown SIPH brown with lighter basal part, cauda and anal plate brown to dark brown (Fig. 1c). HW  $0.34\text{--}0.35 \times \text{ANT}$ . Head setae  $0.015\text{--}0.045$  mm long,  $0.60\text{--}1.00 \times \text{BD III}$ . ANT  $0.65\text{--}0.67 \times \text{BL}$ . ANT IV as long as or longer than ANT V. ANT VI with PT  $3.58\text{--}4.27 \times \text{BASE}$ . Other antennal ratios: VI:III  $2.07\text{--}2.11$ , V:III  $0.61\text{--}0.67$ , IV:III  $0.67\text{--}0.80$ , PT:III  $1.65\text{--}1.67$ , PT:IV  $2.04\text{--}2.47$ , PT:V  $2.47\text{--}2.68$ . ANT bearing long, fine and pointed. ANT III setae as long as and longer than the width of the segment (Fig. 5g),  $0.030\text{--}0.040$  mm long, LS III  $1.20\text{--}2.00 \times \text{BD III}$ . ANT I with 4–5, ANT II with 5, ANT III with 1417, ANT IV with 11–12, ANT V with 7, ANT VI with 2 basal setae. Rostrum reaching from hind coxae to ABD I. URS  $0.57\text{--}0.59 \times \text{ANT III}$ ,  $0.27\text{--}0.28 \times \text{ANT VI}$ ,  $0.34\text{--}0.36 \times \text{PT}$ ,  $1.29\text{--}1.45 \times \text{BASE}$  and  $1.14\text{--}1.19 \times \text{HT II}$ . Mesosternal furca robust, fused and wide. III FEMORA bearing long, fine and pointed setae (Fig 5h),  $0.025\text{--}0.055$  mm long, III FEMORA LS  $1.00\text{--}1.10 \times \text{trochantero-femoral suture length}$ . Posterior seta on hind trochanter about  $0.90 \times \text{trochantero-femoral suture length}$  (Fig. 5i). III TIBIAE bearing long, fine and pointed setae,  $0.050\text{--}0.055$  mm long. HT II about  $0.50 \times \text{ANT III}$ ,  $0.23\text{--}0.24 \times \text{ANT VI}$ ,  $0.29\text{--}0.30 \times \text{PT}$  and  $1.08\text{--}1.27 \times \text{BASE}$ . Abdomen with small marginal tubercles on ABD IV. SIPH about  $1.33 \times \text{cauda}$ ,  $0.09\text{--}0.10 \times \text{BL}$ , and  $0.76\text{--}0.78 \times \text{ANT III}$ . Setae on ABD I–V  $0.010\text{--}$



0.015 mm long,  $0.40\text{--}0.62 \times \text{BD III}$ . Setae on ABD VI–VIII  $0.015\text{--}0.032$  mm long,  $0.70\text{--}0.75 \times \text{BD III}$ . Genital plate anterior setae  $0.060\text{--}0.070$  mm long, about  $3.50 \times \text{BD III}$ . Cauda with 16–17 setae (Fig. 6e, f).

**Remarks:** Despite Huculak (1968) gave short descriptions of oviparous females and males in the original description, no material has been found in the ZMPA collection. The alate viviparous females are unknown. Measurements of the specimens examined in this study vary from those given by Huculak in the original description (1968) and in Blackman & Eastop (2019). The differences are maybe due to the fact that Huculak measured more specimens which were not available for us.

**Material examined.** Holotype: POLAND: Trzebinia, 26 August 1967, on *Knautia arvensis*, L. Olesiński leg., 1 apt, APH-1469, ZMPA; Paratype: the same data as holotype, 1 apt, APH-1479, ZMPA, 1 apt, APH-1477; other material: Trzebinia, 01 October 1967, on *K. arvensis*, L. Olesiński leg., 1 apt. 2651, R621, ZMPA;

**Host plants.** The species is known only from *K. arvensis* (Holman 2009).

**Biology.** It is a monoecious and holocyclic species with sexual generation in October. The aphids form large, ant-attended colonies on the bases of stems on the plant (Huculak 1968).

**Distribution.** Poland, Russia (Holman, 2009). Olesiński & Szelegiewicz (1974) provided that this species was also found in “Czechoslovakia” but without existing material it was impossible to determine if it was the Czech Republic or Slovakia.

*Aphis (Aphis) thomasi* (Börner, 1950)

*Doralina thomasi* Börner, 1950: 7  
Figs 1–7; Supplementary tables 1–4

*Apterous viviparous female* (n=12).

**Colour** in life: straw yellow (Blackman & Eastop, 2019); pigmentation on slide: head sclerotized, light brown. Antennae light brown with pale basal half of ANT III and base of ANT IV. Tibiae of legs light brown with slightly paler basal distal parts, tibiae light brown to pale with light brown apical parts, tarsi light brown. Abdomen yellow with light brown SIPH, cauda and anal plate (Fig. 1d). HW  $0.47\text{--}0.58 \times \text{ANT}$ . Head setae  $0.005\text{--}0.010$  mm long,  $0.25\text{--}0.29 \times \text{BD III}$ . ANT  $0.49\text{--}0.54 \times \text{BL}$ . ANT IV as long as or shorter than ANT V. ANT VI with PT  $2.00\text{--}3.20 \times \text{BASE}$ . Other antennal ratios: VI:III  $1.42\text{--}2.10$ , V:III  $0.50\text{--}0.69$ , IV:III  $0.46\text{--}0.60$ , PT:III  $1.00\text{--}1.60$ , PT:IV  $1.90\text{--}2.66$ , PT:V  $1.66\text{--}2.26$ . ANT bearing very short and blunt setae (Fig. 5j). ANT III setae shorter than the width of the segment,  $0.003\text{--}$

$0.007$  mm long, LS III  $0.25\text{--}0.65 \times \text{BD III}$ . ANT I with 3–6, ANT II with 3–5, ANT III with 4–6, ANT IV with 2–3, ANT V with 1–4, ANT VI with 1–2 basal setae. Rostrum reaching to ABD I. URS  $0.65\text{--}0.80 \times \text{ANT III}$ ,  $0.38\text{--}0.46 \times \text{ANT VI}$ ,  $0.50\text{--}0.70 \times \text{PT}$ ,  $1.40\text{--}1.60 \times \text{BASE}$  and  $1.31\text{--}1.66 \times \text{HT II}$ . Mesosternal furca slightly fused, wide. III FEMORA bearing very short, rigid and blunt setae (Fig. 5k),  $0.005\text{--}0.007$  mm long, III FEMORA LS  $0.12\text{--}0.25 \times \text{trochantero-femoral suture length}$ . Posterior seta on hind trochanter  $0.18\text{--}0.25 \times \text{trochantero-femoral suture length}$  (Fig. 5l). III TIBIAE bearing short rigid and blunt setae,  $0.005\text{--}0.025$  mm long. HT II  $0.43\text{--}0.60 \times \text{ANT III}$ ,  $0.25\text{--}0.35 \times \text{ANT VI}$ ,  $0.37\text{--}0.50 \times \text{PT}$  and  $0.92\text{--}1.20 \times \text{BASE}$ . SIPH  $1.09\text{--}1.60 \times \text{cauda}$ ,  $0.11\text{--}0.16 \times \text{BL}$ , and  $0.80\text{--}1.53 \times \text{ANT III}$ . Setae on ABD I–V  $0.006\text{--}0.010$  mm long,  $0.30\text{--}0.44 \times \text{BD III}$ . Setae on ABD VI–VIII  $0.007\text{--}0.025$  mm long,  $0.37\text{--}0.73 \times \text{BD III}$ . Genital plate anterior setae  $0.010\text{--}0.035$  mm long,  $0.50\text{--}1.47 \times \text{BD III}$ . Cauda with 6–8 setae.

*Alate viviparous female* (n=2).

**Colour** in life: unknown; pigmentation on slide: head sclerotized, brown. Antennae yellow or light brown with paler basal parts of ANT III–VI BASE. Femora of legs uniformly light brown with pale distal parts. Tibiae pale with light brown distal parts of tibiae and light brown tarsi. Abdomen pale with light brown SIPH, cauda and anal plate (Fig. 2c). HW  $0.35\text{--}0.36 \times \text{ANT}$ . Head setae  $0.008\text{--}0.010$  mm long, about  $0.66 \times \text{BD III}$ . ANT  $0.62\text{--}0.65 \times \text{BL}$ . ANT III with 8–10 secondary rhinaria. ANT IV as long as or shorter than ANT V, with 2–4 secondary rhinaria. ANT V sometimes with one secondary rhinarium. ANT VI with PT  $2.30\text{--}2.53 \times \text{BASE}$ . Other antennal ratios: VI:III  $1.43\text{--}1.52$ , V:III  $0.59\text{--}0.65$ , IV:III  $0.56\text{--}0.59$ , PT:III  $1.00\text{--}1.09$ , PT:IV  $1.76\text{--}1.84$ , PT:V  $1.53\text{--}1.84$ . ANT bearing very short and blunt setae. ANT III setae shorter than the width of the segment,  $0.005\text{--}0.010$  mm long, LS III  $0.60\text{--}0.66 \times \text{BD III}$ . ANT I with 4–5, ANT II with 4, ANT III with 5–6, ANT IV with 3–4, ANT V with 3–4, ANT VI with 1–3 basal setae. Rostrum reaching hind coxae. URS  $0.45\text{--}0.50 \times \text{ANT III}$ ,  $0.31\text{--}0.32 \times \text{ANT VI}$ , about  $0.45 \times \text{PT}$ ,  $1.05\text{--}1.15 \times \text{BASE}$  and  $1.22\text{--}1.23 \times \text{HT II}$ . III FEMORA bearing short, rigid and blunt setae,  $0.007\text{--}0.012$  mm long, III FEMORA LS  $0.31\text{--}0.35 \times \text{trochantero-femoral suture length}$ . Posterior seta on hind trochanter  $0.31\text{--}0.39 \times \text{trochantero-femoral suture length}$ . III TIBIAE bearing short rigid and blunt setae,  $0.010\text{--}0.022$  mm long. HT II  $0.36\text{--}0.40 \times \text{ANT III}$ ,  $0.25\text{--}0.26 \times \text{ANT VI}$ ,  $0.36\text{--}0.37 \times \text{PT}$  and  $0.85\text{--}0.94 \times \text{BASE}$ . Abdomen with sclerite on ABD I, large marginal plates on ABD II–IV and small ones on ABD V, which is without presiphuncular sclerites. ABD VI with large postsiphuncular sclerites and very small spinal sclerite. ABD VII with wide spino-pleural plate. ABD I and VII with visible marginal tubercles (Fig. 7c). SIPH  $1.09\text{--}1.61 \times \text{cauda}$ ,  $0.08\text{--}0.11 \times \text{BL}$ , and  $0.54\text{--}0.73 \times \text{ANT III}$ . Setae



on ABD I–V 0.007–0.012 mm long,  $0.50\text{--}0.66 \times \text{BD III}$ . Setae on ABD VI–VIII 0.010–0.017 mm long, about  $0.66 \times \text{BD III}$ . Genital plate anterior setae 0.012–0.015 mm long,  $0.83\text{--}1.00 \times \text{BD III}$ . Cauda with 5–8 setae (Fig. 7c).

*Oviparous female.* Description (n=9).

*Colour* in life: unknown; pigmentation on slide: head sclerotized, light brown. Antennae yellow or light yellow with ANT I, ANT II, ANT V and ANT VI light brown. Femora yellow or light brown with paler proximal parts. Fore and middle tibiae yellow or light brown with darker distal parts and tarsi. Hind tibiae light uniformly light brown or with slightly darker apical half. Abdomen yellow with light brown SIPH, cauda and anal plate (Fig. 3c). HW  $0.51\text{--}0.56 \times \text{ANT}$ . Head setae 0.005–0.011 mm long,  $0.28\text{--}0.37 \times \text{BD III}$ . ANT  $0.44\text{--}0.48 \times \text{BL}$ . ANT IV as long as or slightly shorter than ANT V. ANT VI with PT  $2.13\text{--}2.56 \times \text{BASE}$ . Other antennal ratios: VI:III 2.35–2.59, V:III 0.75–0.81, IV:III 0.60–0.81, PT:III 1.60–1.86, PT:IV 2.27–2.66, PT:V 2.00–2.27. ANT bearing very short and blunt setae. ANT III setae shorter than the width of the segment, 0.005–0.075 mm long, LS III  $0.28\text{--}0.58 \times \text{BD III}$ . ANT I with 4–6, ANT II with 3–5, ANT III with 3–5, ANT IV with 3, ANT V with 3–4, ANT VI with 2–3 basal setae. Rostrum reaching hind coxae. URS  $0.91\text{--}1.10 \times \text{ANT III}$ ,  $0.36\text{--}0.46 \times \text{ANT VI}$ ,  $0.51\text{--}0.68 \times \text{PT}$ ,  $1.29\text{--}1.46 \times \text{BASE}$  and  $1.31\text{--}1.46 \times \text{HT II}$ . Mesosternal poorly visible almost separated. III FEMORA bearing very short, rigid and blunt setae, 0.005–0.010 mm long, III FEMORA LS  $0.15\text{--}0.23 \times \text{trochantero-femoral suture length}$ . Posterior seta on hind trochanter about  $0.17 \times \text{trochantero-femoral suture length}$ . III TIBIAE with 27–53 pseudosensoria, bearing short to medium in length, rigid and blunt setae, 0.007–0.022 mm long. HT II  $0.66\text{--}0.75 \times \text{ANT III}$ ,  $0.28\text{--}0.31 \times \text{ANT VI}$ ,  $0.39\text{--}0.46 \times \text{PT}$  and  $0.94\text{--}1.00 \times \text{BASE}$ . SIPH  $1.13\text{--}1.33 \times \text{cauda}$ ,  $0.10\text{--}0.11 \times \text{BL}$ , and  $1.25\text{--}1.50 \times \text{ANT III}$ . Setae on ABD I–V 0.005–0.008 mm long, about  $0.25\text{--}0.42 \times \text{BD III}$ . Setae on ABD VI–VIII 0.010–0.017 mm long,  $0.50\text{--}0.80 \times \text{BD III}$ . Genital plate anterior setae 0.017–0.020 mm long,  $0.87\text{--}1.14 \times \text{BD III}$ . Cauda with 6–10 setae.

*Male.* Description (n=1).

*Colour* in life: unknown; pigmentation on slide: head sclerotized, light brown. Antennae light brown with paler basal part of ANT III. Legs yellow with lighter central parts of tibiae. Abdomen pale, SIPH light brown with paler basal parts, cauda and anal genitalia light brown (Fig. 4c). HW  $0.49\text{--}0.52 \times \text{ANT}$ . Head setae 0.008–0.010 mm long, about  $0.40 \times \text{BD III}$ . ANT 5-segmented,  $0.57\text{--}0.60 \times \text{BL}$ . ANT III with 10, ANT IV with 1–3 secondary rhinaria. ANT V with PT  $2.28\text{--}3.00 \times \text{BASE}$ . Other antennal ratios: V:III 1.45–1.48, IV:III 0.48–0.51, PT:III 1.03–1.09, PT:IV 2.00–2.25. ANT bearing very short and blunt setae. ANT III setae shorter than the width of the segment, 0.005–0.006 mm long, LS III

$0.30\text{--}0.50 \times \text{BD III}$ . ANT I with 5, ANT II with 4, ANT III with 5–6, ANT IV with 3–4, ANT V with 1–2 basal setae. Rostrum reaching ABD III. URS  $0.60\text{--}0.64 \times \text{ANT III}$ ,  $0.41\text{--}0.43 \times \text{ANT VI}$ ,  $0.55\text{--}0.62 \times \text{PT}$ ,  $1.42\text{--}1.66 \times \text{BASE}$  and about  $1.42 \times \text{HT II}$ . Mesosternal furca poorly visible, separated. III FEMORA bearing very short, rigid and blunt setae, 0.005–0.007 mm long, III FEMORA LS about  $0.16 \times \text{trochantero-femoral suture length}$ . Posterior seta on hind trochanter about  $0.22 \times \text{trochantero-femoral suture length}$ . III TIBIAE bearing short, rigid and blunt setae, 0.005–0.017 mm long. HT II  $0.42\text{--}0.45 \times \text{ANT III}$ ,  $0.29\text{--}0.30 \times \text{ANT V}$ ,  $0.38\text{--}0.43 \times \text{PT}$  and  $1.00\text{--}1.16 \times \text{BASE}$ . Abdomen with small marginal tubercles on ABD IV. SIPH  $1.00\text{--}1.10 \times \text{cauda}$ ,  $0.10\text{--}0.11 \times \text{BL}$ , and  $0.64\text{--}0.66 \times \text{ANT III}$ . Setae on ABD I–V 0.007–0.010 mm long,  $0.37\text{--}0.50 \times \text{BD III}$ . Setae on ABD VI–VIII 0.010–0.015 mm long,  $0.50\text{--}0.75 \times \text{BD III}$ . Cauda with 6 setae.

**Material examined.** BULGARIA: Liljanovo (10 km E of Sandenski) reg. Blagoevgrad, 28 May 1990, on *Scabiosa* sp., J. Holman leg., 4 apt, 21840 A (apt. 1–4), IECA; CZECH REPUBLIC: Luka p. Mednikem, 30 September 1964, on *S. canescens*, J. Holman leg., 7 ♀, 8851 (♀ 9–15), IECA; POLAND: Augustów, 05 July 1967, on *S. ochroleuca*, S. Huculak leg., 1 apt, 1248, R838; ZMPA; Warszawa-Bielany, 30 September 1965, on *S. ochroleuca*, H. Szelegiewicz leg., 5 apt, 2991, R839, ZMPA; 2 apt, 2♀, 1 ♂, 2991, R839, 363, ZMPA; UKRAINE: Čatyrdag, Krimea, 21 July 1960, on *S. gramuntia* (= *S. trandria*), J. Holman leg., 2 al, 3898 (al. 1–2), IECA.

**Host plants.** *Knautia arvensis*, *Scabiosa* sp., *S. argentea*, *S. atropurpurea*, *S. canescens*, *S. columbaria*, *S. comosa* (= *S. lachnophylla*), *S. ochroleuca*, *S. triandra* (Holman, 2009), *Pycnocomon rutifolium* (Blackman & Eastop 2019).

**Biology.** *Aphis thomasi* is a monoecious and holocyclic species with sexual phase in the end of September. The aphids live on basal parts on the host plants.

**Distribution.** Bulgaria, Czech Republic, Germany, Poland, Romania, Slovakia, Spain, Switzerland, Ukraine, probably Hungary (de Jong et al. 2014).

**Key to *Knautia* feeding *Aphis* based on Blackman & Eastop (2019)**

- 1 ANT tubercles undeveloped or weakly developed. ABD TERG 1 and 7 with marginal tubercles (MTu) ..... 2
- ANT tubercles well developed. ABD TERG 1 and 7 without MTu..... 4
2. Cauda with 14–24 hairs. Longest hairs on hind femur as long as or longer than diameter of trochantero-femoral suture. Well-developed MTu present on



- ABD TERG 2–4 as well as 1 and 7. ANT PT/BASE 3–4..... *Aphis longini*
- Cauda with 4–9 hairs. Longest hairs on hind femur 0.15–0.7 of diameter of trochantero-femoral suture. Small MTu present or absent from ABD TERG 2–4(–5). ANT PT/BASE 1.5–3.3 ..... **3**
3. Posterior hair on hind trochanter 0.2–0.5 × diameter of trochantero-femoral suture. Hairs on anterior half of subgenital plate 0.2–0.5 × ANT BD III ..... *Aphis thomasi*
- Posterior hair on hind trochanter 0.6–1.1 × diameter of trochantero-femoral suture. Hairs on anterior half of subgenital plate 1.0–3.0 × ANT BD III ..... **4**
4. Hairs on hind femora and antennae pointed. Hairs on anterior half of subgenital plate 2.25–2.94 × Ant BD III, R IV+V 1.40–1.52 × HT II..... *Aphis holmani* sp. nov.
- Hairs on hind femora and antennae with blunt apices. Hairs on anterior half of subgenital plate 1.00–2.00 × Ant BD III, R IV+V 0.90–1.10 × HT II ..... *Aphis confusa*
5. Head and SIPH black. ANT III with 7–25 rhinaria. SIPH with polygonal reticulation on distal 0.1–0.2 of length (8 or more rows of closed cells)..... **5**
- Head and SIPH pale. ANT III with 0–3 rhinaria. SIPH without polygonal reticulation or with only 1–4 rows of closed cells ..... **6**

**Acknowledgements.** We would like to thank the editor and two anonymous referees for valuable comments and suggestions which greatly improved the first version of the manuscript. Mariusz Kanturski gratefully acknowledges the Scholarship for Outstanding Young Scientists from the Ministry of Science and Higher Education of Poland (1165/E-340/STYP/12/17). Aleš Bezděk was partially supported by the research program Strategy AV21 of the Czech Academy of Sciences – Diversity of Life and Health of Ecosystems”.

## REFERENCES

- Blackman RL, Eastop VF (2006) Aphids on the World's Herbaceous Plants and Shrubs. John Wiley & Sons, Ltd., West Sussex, 1439 pp.
- Blackman RL, Eastop VF (2019) Aphids on the World's Plants. An online identification and information guide. <http://www.aphidsonworldsplants.info> (last access on June 15, 2019)
- Börner C (1950) Neue europäische Blattläusarten. Naumburg (privately published), 19 pp.
- Ehrendorfer F (1962) Beiträge zur Phylogenie der Gattung *Knautia* (Dipsacaceae), I. Cytologische Grundlagen und allgemeine Hinweise. Österreichische Botanische Zeitschrift 109: 276–343
- Ehrendorfer F (1976) *Knautia* L. Pp. 60–67 in: Tutin T, Heywood VH, Burges NA, Valentine DH (eds) Flora Europaea, vol. 4. Cambridge University Press, Cambridge
- Favret C (2019) Aphid Species File. Version 5.0/5.0. <http://www.Aphid.SpeciesFile.org> (last access on June 15, 2019)

- Fischer MA, Oswald K, Adler W (2008) Exkursionsflora für Österreich, Liechtenstein und Südtirol, 3<sup>rd</sup> ed. Biologiezentrum der Oberösterreichischen Landesmuseen, Linz, Austria, 1391 pp.
- Heie OE (1986) The Aphidoidea (Hemiptera) of Fennoscandia and Denmark III. Pterocommatinae and Aphidinae, Aphidini. Fauna Entomologica Scandinavica 17: 1–314
- Holman J, Pintera A (1981) Übersicht der Blattläuse (Homoptera, Aphidoidea) der Rumänischen Sozialistischen Republik. Studie ČSAV (Prague) 15: 1–125
- Holman J (2009) Host Plant Catalog of Aphids, Palearctic Region. Springer Science + Business Media B.V., 1216 pp
- Huculak S (1968) Eine neue Art der Gattung *Aphis* L. (Homoptera, Aphididae) am *Knautia arvensis* (L.) Coult. aus Polen. Annales Zoologici XXVI: 333–342
- Ilharco FA, van Harten A (1987) Systematics. In: Minks AK & Harrewijn P (eds) Aphids: their biology, natural enemies and control. Elsevier Science Publishers, Amsterdam: 51–77
- ICZN [International Commission on Zoological Nomenclature] (1999) International Code of Zoological Nomenclature. 4th Edition. The International Trust for Zoological Nomenclature, London, 306 pp
- Jong Y de, Verbeek M, Michelsen V, Bjørn P, Los W, Steeman F, Bailly N, Basire C, Chylarecki P, Stloukal E, Hagedorn G, Wetzel F, Glöckler F, Kroupa A, Korb G, Hoffmann A, Häuser C, Kohlbecker A, Müller A, Güntsch A, Stoev P, Penev L (2014) Fauna Europaea – all European animal species on the web. Biodiversity Data Journal 2: e4034. <https://doi.org/10.3897/BDJ.2.e4034>
- Olesiński L, Szelegiewicz H (1974) Mszyce (Homoptera, Aphidodea) okolic Chrzanowa. Fragmenta Faunistica XIX (12): 319–347
- Rešetnik I, Frajman B, Bogdanović S, Ehrendorfer F, Schönswetter P (2014) Disentangling relationships among the diploid members of the intricate genus *Knautia* (Caprifoliaceae, Dipsacaceae). Molecular Phylogenetics and Evolution 74: 97–110
- Rešetnik I, Frajman B, Schönswetter P (2016) Heteroploid *Knautia drymeia* includes *K. gussonei* and cannot be separated into diagnosable subspecies. American Journal of Botany 103(7): 1300–1313
- Walker F (1849) Descriptions of new British Aphides. The Zoologist 7 (appendix): xliii–lvii

## APPENDIX I

(electronic supplement, available at [www.bonnzoologicalbulletin.de](http://www.bonnzoologicalbulletin.de))

**Suppl. table 1.** Measurements (in mm) of apterous viviparous females of *Knautia* feeding *Aphis* species; \*measurements of ANT III for specimens with 5-segmented antennae. \*\*measurements of ANT III for specimens with 6-segmented antennae.

**Suppl. table 2.** Measurements (in mm) of known alate viviparous females of *Knautia* feeding *Aphis* species.

**Suppl. table 3.** Measurements (in mm) of available for examination oviparous females of *Knautia* feeding *Aphis* species.

**Suppl. table 4.** Measurements (in mm) of available for examination males of *Knautia* feeding *Aphis* species (male of *A. thomasi* with 5-segmented antennae).



BHL



Blank Page Digitally Inserted



APPENDIX 1

**Suppl. table 1.** Measurements (in mm) of apterous viviparous females of *Knautia* feeding *Aphis* species.  
\*measurements of ANT III for specimens with 5-segmented antennae; \*\*measurements of ANT III for specimens with 6-segmented antennae.

Character	<i>Aphis confusa</i>	<i>Aphis holmani</i> sp. nov.	<i>Aphis longini</i>	<i>Aphis thomasi</i>
BL	1.75–2.07	1.50–2.00	2.00–2.10	1.20–1.55
MAX W	0.87–1.32	0.85–1.25	1.25–1.32	0.71–0.92
HW	0.36–0.45	0.38–0.44	0.48–0.49	0.35–0.38
ANT	0.94–1.21	0.85–1.20	1.35–1.41	0.59–0.78
ANT III	0.22–0.32	0.29–0.38*	0.17	0.13–0.15*
		0.24–0.33**		0.13–0.19**
ANT IV	0.14–0.19	0.13–0.19	0.19–0.21	0.06–0.10
ANT V	0.14–0.18	0.14–0.19	0.16–0.19	0.09–0.11
ANT VI	0.32–0.39	0.30–0.37	0.55–0.58	0.22–0.31
BASE	0.08–0.11	0.10–0.13	0.11–0.12	0.070–0.080
PT	0.24–0.28	0.20–0.24	0.43–0.47	0.15–0.24
URS	0.10–0.12	0.13–0.16	0.15–0.16	0.105–0.125
III FEMUR	0.37–0.50	0.35–0.49	0.48–0.50	0.23–0.34
III FEMUR LS	0.030–0.035	0.045–0.050	0.050–0.055	0.010–0.011
PHT	0.035–0.050	0.050–0.055	0.050	0.010–0.012
III TIBIA	0.69–0.93	0.64–0.94	0.92–0.95	0.44–0.60
HT II	0.09–0.12	0.085–0.100	0.13–0.14	0.075–0.095
SIPH	0.24–0.38	0.18–0.27	0.20–0.22	0.20–0.24
CAUDA	0.15–0.21	0.15–0.18	0.18–0.18	0.13–0.15
GPL	0.10–0.13	0.11–0.12	0.14–0.16	0.090–0.100
GPW	0.20–0.26	0.22–0.43	0.27–0.29	0.19–0.20



**Suppl. table 2.** Measurements (in mm) of known alate viviparous females of *Knautia* feeding *Aphis* species.

Character	<i>Aphis confusa</i>	<i>Aphis holmani</i> sp. nov.	<i>Aphis thomasi</i>
BL	1.55–1.70	1.20–1.57	1.42–1.50
MAX W	0.72–0.80	0.50–0.66	0.50–0.60
HW	0.36–0.37	0.30–0.34	0.33–0.35
ANT	1.015–1.055	0.920–1.035	0.92–0.94
ANT III	0.22–0.26	0.21–0.26	0.22–0.23
ANT IV	0.15–0.18	0.13–0.15	0.13
ANT V	0.15–0.17	0.14–0.15	0.13–0.15
ANT VI	0.34–0.39	0.34–0.36	0.33
BASE	0.10–0.11	0.100–0.105	0.095–0.100
PT	0.24–0.29	0.24–0.26	0.23–0.24
URS	0.10–0.11	0.125–0.135	0.105–0.110
III FEMUR	0.38–0.42	0.34–0.40	0.31–0.32
III FEMUR LS	0.022–0.025	0.032–0.035	0.010–0.012
PHT	0.015–0.030	0.032–0.037	0.011–0.012
III TIBIA	0.75–0.81	0.72–0.80	0.61–0.65
HT II	0.085–0.100	0.080–0.090	0.085–0.090
SIPH	0.21–0.23	0.12–0.15	0.12–0.17
CAUDA	0.13–0.15	0.10–0.11	0.105–0.110
GP L	0.09–0.10	0.08–0.10	0.08–0.10
GP W	0.18–0.20	0.18–0.22	0.18–0.20



**Suppl. table 3.** Measurements (in mm) of available for examination oviparous females of *Knautia* feeding *Aphis* species.

Character	<i>Aphis confusa</i>	<i>Aphis holmani</i> sp. nov.	<i>Aphis thomasi</i>
<b>BL</b>	1.45–1.52	1.45–1.60	1.25–1.52
<b>MAX W</b>	0.70–0.79	0.80–0.92	0.60–1.02
<b>HW</b>	0.33–0.37	0.36–0.38	0.30–0.38
<b>ANT</b>	0.70–0.73	0.77–0.85	0.57–0.68
<b>ANT III</b>	0.12–0.14	0.13–0.16	0.10–0.12
<b>ANT IV</b>	0.09–0.10	0.11–0.13	0.06–0.09
<b>ANT V</b>	0.11–0.12	0.12–0.14	0.08–0.09
<b>ANT VI</b>	0.28	0.29–0.32	0.23–0.28
<b>BASE</b>	0.08	0.08	0.075–0.085
<b>PT</b>	0.20	0.21–0.24	0.16–0.20
<b>URS</b>	0.09–0.10	0.11	0.10–0.11
<b>III FEMUR</b>	0.26–0.30	0.29–0.32	0.20–0.26
<b>III FEMUR LS</b>	0.025–0.035	0.04–0.05	0.007–0.010
<b>PHT</b>	0.027–0.045	0.037–0.050	0.007–0.010
<b>III TIBIA</b>	0.46–0.51	0.54–0.60	0.38–0.46
<b>HT II</b>	0.075–0.080	0.08–0.09	0.075–0.08
<b>SIPH</b>	0.16–0.18	0.13–0.14	0.12–0.16
<b>CAUDA</b>	0.13–0.14	0.12–0.13	0.11–0.13
<b>GPL</b>	0.10–0.11	0.10–0.12	0.12–0.13
<b>GP W</b>	0.23–0.25	0.24–0.28	0.20–0.25



**Suppl. table 4.** Measurements (in mm) of available for examination males of *Knautia* feeding *Aphis* species (male of *A. thomasi* with 5-segmented antennae).

Character	<i>Aphis confusa</i>	<i>Aphis holmani</i> sp. nov.	<i>Aphis thomasi</i>
BL	1.00–1.05	0.80–1.07	0.97
MAX W	0.46–0.57	0.43–0.55	0.46
HW	0.31–0.33	0.27–0.34	0.29
ANT	0.76–0.84	0.85–0.93	0.55–0.58
ANT III	0.17	0.17–0.18	0.155–0.165
ANT IV	0.10–0.12	0.14–0.16	0.08
ANT V	0.13–0.14	0.14–0.15	–
ANT VI	0.28–0.31	0.30–0.33	0.23–0.24
BASE	0.07–0.08	0.07–0.08	0.06–0.07
PT	0.20–0.22	0.23–0.25	0.16–0.17
URS	0.085	0.09–0.10	0.10
III FEMUR	0.23–0.25	0.26–0.27	0.21
III FEMUR LS	0.025–0.032	0.032–0.040	0.0075
PHT	0.040–0.045	0.032–0.037	0.01
III TIBIA	0.45–0.50	0.52–0.56	0.39
HT II	0.065–0.070	0.070–0.075	0.07
SIPH	0.10–0.11	0.08–0.09	0.10–0.11
CAUDA	0.09–0.10	0.09–0.10	0.10



# Scientific note

urn:lsid:zoobank.org:pub:0D573D65-6DD1-4B3C-9ED9-D44F48638C54

## First record of males of the invasive eucalyptus pest species *Leptocybe invasa* Fisher & LaSalle, 2004 (Hymenoptera: Eulophidae: Tetrastichinae) from South America

Daniel Alejandro Aquino<sup>1,\*</sup>, Carmen Marcela Hernández<sup>2</sup> & Andrea Verónica Andorno<sup>3</sup>

<sup>1</sup>Centro de Estudios Parasitológicos y de Vectores (CEPAVE, CONICET-UNLP), Boulevard 120 entre 60 y 64,  
AR-1900 La Plata, Argentina

<sup>2,3</sup>Instituto Nacional de Tecnología Agropecuaria (INTA). Instituto de Microbiología y Zoología Agrícola, AR-Argentina

\*Corresponding author: Email: [daquino@fcnym.unlp.edu.ar](mailto:daquino@fcnym.unlp.edu.ar)

<sup>1</sup>urn:lsid:zoobank.org:author:670E065F-04CF-4247-8515-AC41D151017A

<sup>2</sup>urn:lsid:zoobank.org:author:778230C8-8EA2-4C21-892B-ACB488810D25

<sup>3</sup>urn:lsid:zoobank.org:author:47B448E3-6B06-4343-BB2F-8E87D4E17750

**Abstract.** The “blue gum chalcid”, *Leptocybe invasa* is a pest of eucalyptus worldwide. It has an Australian origin and has expanded into Asia, Europe, Africa and America. *L. invasa* females were reported from South America in the last decade. Thelytokous parthenogenesis is the most common reproductive mechanism of this pest. However, male adults have been reported from Asia and Southeastern Europe. In this work, *L. invasa* males are reported for the first time from South America (Argentina) and information on morphological characters of males is provided. The importance of this discovery is highlighted based on recent studies that suggested the existence of two cryptic *Leptocybe* species in invasive populations.

**Key words.** Blue gum chalcid, gall, forest, chalcidoidea.

The “blue gum chalcid”, *Leptocybe invasa* Fisher & LaSalle, 2004 (Hymenoptera: Eulophidae: Tetrastichinae) is a global pest in *Eucalyptus* plantations. The wasp lays eggs in plant tissues causing the formation of galls on the midribs, petioles and stems of young leaves. Severely infested trees have a gnarled appearance, show stunted growth, and in young trees, this pest can cause significant injury (Mendel et al. 2004; Nyeko, 2005).

The rapid colonization after *L. invasa* spread into a novel environment can be attributed to the absence of natural enemies, the presence of large amounts of suitable host plants, the resistance to low temperatures of adults and the occurrence of two reproductive modes (Zheng et al. 2014b). This pest displays thelytokous reproduction but since the discovery of males, sexual reproduction has been considered a second reproductive strategy. Nevertheless, factors influencing reproductive strategies and the relation between reproductive strategy and population expansion are unknown (Zheng et al. 2014a). In the current study, we describe male specimens of *L. invasa* from Argentina and report the sex ratio in eucalyptus plantations in the country.

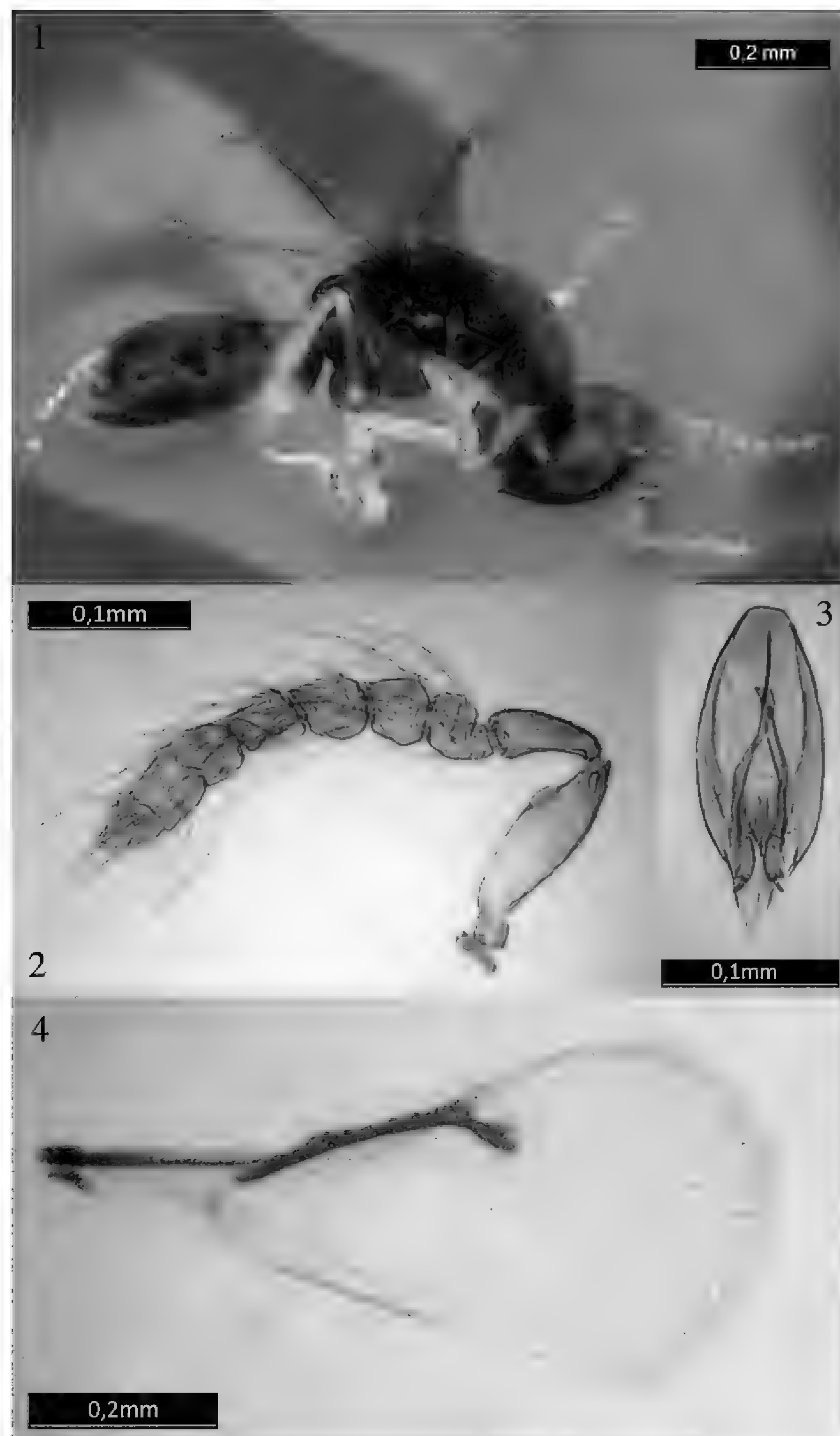
In 2017 and 2018, a survey of *L. invasa* populations and natural enemies was conducted in infested eucalyptus plantations in an extensive productive area in Buenos Aires and the Mesopotamia region (Entre Ríos, Corrientes and Misiones). Almost fifty samples of 20–30 cm

long, *L. invasa* gall infested branches were collected. The plant material was kept in glass containers with voile lid and absorbent paper under controlled laboratory conditions (T: 25 ± 2°C, HR: 50–70% and natural lighting). The insects that emerged from each sample were kept in 70% ethanol and were identified by the first author. The specimens were card- and slide-mounted following Noyes (1990) and were compared with the descriptions of the males in Doğanlar (2005), Chen et al. (2009) and Zheng et al. (2014b). Voucher specimens were deposited at the División Entomología of Museo de La Plata. Sex ratios were calculated as  $\Sigma \text{♀} / \Sigma (\text{♀} + \text{♂})$ . Measurements were taken with a Leitz Wetzlar SM/LUX; specimens were photographed using a Leica DFC295 digital camera attached to a stereomicroscope Biotraza. Series of partially focused digital images were stacked using the Helicon Focus software (Version 6.8.0 Pro) by ©Helicon Soft Ltd., 2000. Photoshop CC2018 was used to produce final images with enhanced quality.

**Material examined.** Argentina, Entre Ríos, Concordia en 8.iii.2018 and 5.x.2018 (sex ratio 3m:104f (0,972) and 17m:1290f (0.987)); Argentina, Corrientes, Alvear 28.ix.2018 (sex ratio 1m:24f (0,960)).

According to Doğanlar (2005), the male is similar to the female described by Fisher & LaSalle (2004), except:





**Figs. 1–4.** *Leptocybe invasa* male from Argentina. 1. lateral habitus; 2. antenna; 3. genitalia; 4. forewing.

head and mesosoma brown with distinct blue to green metallic shine (Fig. 1); ocellar triangle and mouth margin light brown; eyes and ocellus red; malar sulcus dark brown; metasoma brown; legs almost white, except mid and hind coxae same color of the body and hind femur light brown. Antenna with scape and pedicel light brown darkened dorsally and apically; funicle and clava light brown to almost white. Wings hyaline, veins light brown (Fig. 4). Genitalia (Fig. 3) with digitus having one claw. The specimens collected in this study are similar to those described by Doğanlar (2005) except for the following measurements and ratios: Head 1.28 times as broad as high. Antenna (Fig. 2) with scape 3.13 times as long as broad, ventral plaque 0.18–0.24x length of scape; pedicel 1.9–2.8x as long as broad, longer than anelli plus F1; F1 shorter than F2 (in figure 1b in Doğanlar (2005) it is observable that F1 is shorter than F2 although he mentions

that “F1 is 1.46x longer than F2”), about 0.75x length of F2, as long as broad to 0.7 times as long as broad, F2 to F4 subequal in length, each slightly longer than broad; clava about 2.75 times as long as broad, i.e., slightly longer than that described by Doğanlar (2005), with C1–C3 decreasing in length, except in one specimen in which C1 is shorter than C2 and C3.

*Leptocybe invasa* males were reported from Turkey, China, India, Taiwan and Thailand, and populations of this pest around the world are known to have different sex ratios over their geographic distribution (Nugnes et al. 2015). Males are rare in Turkey (sex ratio: 0,992, n=125) (Doğanlar 2005) and India (sex ratio: 0,992, n=141) (Akhtar et al. 2012). In China a low proportion of males was reported from Fujian, Guangdong, Hainan, Guangxi, Jiangxi and Sichuan (sex ratio  $\geq 0,95$ ), but a high proportion of males was reported from other regions (males proportion ranging from 18–48%) and in Thailand (sex ratio: 0,663) (Liang et al. 2010; Santongprow et al. 2011; Zheng et al. 2018).

In this work, in only two out of twenty sampling sites males were found (in Entre Ríos and in Corrientes) and a clearly female-biased sex ratio was found, with values  $\geq 0,96$ .

While *L. invasa* females were recorded from several countries in America since 2007 (Brazil (2007), Argentina (2009), Paraguay (2012), Uruguay (2013), Chile (2014), Mexico (2014) and USA (2008) (Costa et al. 2008; Wiley and Skelley, 2008; Aquino et al. 2011; SAG 2014; Benítez et al. 2014; Vanegas et al. 2015; Jorge et al. 2016)), this is the first report of *L. invasa* males from America. Recent molecular analyses suggested that *L. invasa* is, in fact, a complex of at least two cryptic species involved in the rapid and efficient spread of the wasp (Nugnes et al. 2015; Dittrich-Schröder et al. 2018). Nugnes et al. (2015) proposed that there is a link between the presence of males in the invasive range and lineage identity. Further molecular analyses are necessary to understand the invasion pathways and to characterize the populations of *Leptocybe* species in Argentina and other countries in America.

**Acknowledgements.** The authors thank Sergio Ramos, Cintia Meneses and Edgar Eskiviski for providing samples. We gratefully acknowledge to CONICET and the financial support from PICT-2016-0834 (FONCYT, MINCYT, Argentina).

## REFERENCES

- Akhtar MS, Patankar NV, Gaur A (2012) Observations on the biology and male of eucalyptus gall wasp *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae). Indian Journal of Entomology 74: 173–175
- Aquino DA, Botto EN, Loíacono MS, Pathauer P (2011) Avispa de la agalla del Eucalipto, *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae: Tetrastichinae) en Argentina. Revista de Investigaciones Agropecuarias 37 (2): 159–164



- Benítez EA, Costa VA, de Moraes GJ, Godziewsky D (2014) First record of *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae) and *Rhombacus eucalypti* Ghosh & Chakrabarti (Acari: Eriophyidae) from Paraguay. Boletín del Museo Nacional de Historia Natural de Paraguay 18: 129–132
- Chen HY, Yao JM, Xu ZF (2009) First description of the male of *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae) from China. Journal of Environmental Entomology 31: 285–287 (in Chinese with English abstract)
- Costa VA, Filho EB, Wilcken CF, Stape JL, LaSalle J, Teixeira L (2008) *Eucalyptus* gall wasp, *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae) in Brazil: New forest pest reaches the New World. Revista de Agricultura 83: 136–139
- Dittrich-Schröder G, Hoareau TB, Hurley BP, Wingfield MJ, Lawson S, Nahrung HF, Slippers B (2018) Population genetic analyses of complex global insect invasions in managed landscapes: a *Leptocybe invasa* (Hymenoptera) case study. Biological Invasions 20: 2395
- Doğanlar O (2005) Occurrence of *Leptocybe invasa* Fisher & LaSalle, 2004 (Hymenoptera: Chalcidoidea: Eulophidae) on *Eucalyptus camaldulensis* in Turkey, with description of the male sex. Zoology in the Middle East 35: 112–114
- Jorge C, Martínez G, Gómez D, Bollazzi M (2016) First record of the eucalypt gall-wasp *Leptocybe invasa* (Hymenoptera: Eulophidae) from Uruguay. BOSQUE 37(3): 631–636
- Kumari KN, Kulkarni H, Vastrad AS, Goud KB (2010) Biology of eucalyptus gall wasp, *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae). Karnataka Journal of Agricultural Sciences 23: 211–212
- Liang YP, Li JY, Wen XJ, Li YX (2010) Observation on the male ratio of *Leptocybe invasa* adult. Forest Pest and Disease 29: 21–22 (in Chinese with English abstract).
- Mendel Z, Protasov A, Fisher N, LaSalle J (2004) Taxonomy and biology of *Leptocybe invasa* gen. & sp. n. (Hymenoptera: Eulophidae), an invasive gall inducer on eucalyptus. Australian Journal of Entomology 43: 101–113
- Nugnes F, Gebiola M, Monti MM, Gualtieri L, Giorgini M, Wang JG, Bernardo U (2015) Genetic diversity of the invasive gall wasp *Leptocybe invasa* (Hymenoptera: Eulophidae) and of its Rickettsia endosymbiont, and associated sex ratio differences. PLoS One 10(5): e0124660. <https://doi.org/10.1371/journal.pone.0124660>
- SAG (Servicio Agrícola y Ganadero, CL) (2014) *Leptocybe invasa* Fischer & LaSalle (Hymenoptera: Eulophidae) Microavispa formadora de agallas en eucalipto. Servicio Agrícola y Ganadero. <https://www.sag.gob.cl/ambitos-de-accion/leptocybe-invasa-fischer-lasalle-hymenoptera-eulophidae-microavispa-formadora-de>
- Sangtongpraow B, Charernsom K, Siripatanadilok S (2011) Longevity, fecundity and development time of Eucalyptus gall wasp, *Leptocybe invasa* Fisher and LaSalle (Hymenoptera: Eulophidae) in Kanchanaburi province, Thailand. Thai Journal of Agricultural Science 44: 155–163
- Tung GS, LaSalle J (2010) Pest alert – a newly discovered invasion of gall forming wasps, *Leptocybe invasa* Fisher & LaSalle, on eucalyptus trees in Taiwan. Formosan Entomology 30: 241–244
- Vanegas-Rico JM, Lomeli-Flores JR, Rodríguez-Leyva E, Jiménez-Quiroz E, Pujade-Villar J (2015) First record of eucalyptus gall wasp *Leptocybe invasa* (Hymenoptera: Eulophidae) in Mexico. Revista Mexicana de Biodiversidad 86(4): 1095–1098
- Wiley J, Skelley PA (2008) A eucalyptus pest, *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae), genus and species new to Florida and North America. Pest Alert. Florida, USA: Florida Department of Agriculture and Consumer Services, Division of Plant Industry. [http://www.freshfromflorida.com/content/download/68487/1614796/Pest\\_Alert\\_-\\_Leptocybe\\_invasa\\_Blue\\_Gum\\_Chalcid.pdf](http://www.freshfromflorida.com/content/download/68487/1614796/Pest_Alert_-_Leptocybe_invasa_Blue_Gum_Chalcid.pdf)
- Zheng X, Huang Z, Li J, Yang Z, Lu W (2018) Reproductive Biology of *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae). Neotropical Entomology 47(1): 19–25
- Zheng XL, Li J, Yang ZD, Xian ZH, Wei JG, Lei CL, Wang XP, Lu W (2014a) A review of invasive biology, prevalence and management of *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae: Tetrastichinae). African Entomology 22: 68–79
- Zheng XL, Yang ZD, Li J, Xian ZH, Yang J, Liu JY, Su S, Wang XL, Lu W (2014b) Rapid identification of both sexes of *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae: Tetrastichinae): a morphological perspective. African Entomology 22(3): 643–650



BHL



Blank Page Digitally Inserted



## Research article

urn:lsid:zoobank.org:pub:70A02482-0040-4136-ABB0-9C840A4D771A

# New conopid records from the Afrotropical Region (Diptera) – Part 3: Physocephalini

Jens-Hermann Stuke<sup>1,\*</sup> & David K. Clements<sup>2</sup>

<sup>1</sup> Roter Weg 22, D-26789 Leer, Germany

<sup>2</sup> 7 Vista Rise, Llandaff, Cardiff, CF5 2SD, U.K.

\*Corresponding author: Email: [jstuke@zfn.uni-bremen.de](mailto:jstuke@zfn.uni-bremen.de)

<sup>1</sup>urn:lsid:zoobank.org:author:27ED8CBD-9201-4983-8FE3-698FB499A0E0

<sup>2</sup>urn:lsid:zoobank.org:author:18B2580D-BA69-4BAC-95BE-A519F880D9B3

**Abstract.** The tribe Physocephalini in the Afrotropical Region is now taken to include only the genus *Physocephala*: both *Pseudophysocephala* Kröber, 1940 and *Dacops* Speiser, 1923 are herewith treated as junior subjective synonyms of *Physocephala* Schiner, 1861. Some 45 *Physocephala* species are recorded in the region. Three species are new to science, comprising *P. guillarmodi* spec. nov. (Burundi, Lesotho, South Africa), *P. ssymanki* spec. nov. (Namibia) and *P. goergeni* spec. nov. (Togo). Eighteen new synonyms are introduced: *P. antiqua* (Wiedemann, 1830) = *P. maculipes* (Bigot, 1887) syn. nov. = *P. madagascariensis* Kröber, 1915 syn. nov. = *P. gracilia* Kröber, 1915 syn. nov. = *P. minutissima* Kröber, 1933 syn. nov.; *P. larvata* (Speiser, 1911) = *P. similis* Kröber 1915 syn. nov.; *P. abyssinica* Kröber, 1915 = *P. fumivena* Camras, 2001 syn. nov. = *P. longithecra* Camras, 2001 syn. nov. = *P. atronata* Camras, 2001 syn. nov.; *P. digitata* (Speiser, 1909) = *P. simplex* Kröber, 1915 syn. nov. = *P. ugandae* Kröber, 1915 syn. nov. = *P. bequaertorum* Camras, 1962 syn. nov. = *P. lineifrons* Camras, 1962 syn. nov. = *P. ethiopica* Camras, 1962 syn. nov.; *P. microvena* Brunetti, 1925 = *P. nigratarsis* (Kröber, 1939) syn. nov.; *P. vitripennis* Curran, 1928 = *P. intermedia* Kröber, 1936 syn. nov. = *P. bouvieri* (Séguy, 1936) syn. nov. = *P. meii* Camras, 2001 syn. nov.; *P. nigrita* (Camras, 1962) = *P. brevivertex* (Camras, 2001) syn. nov. *Physocephala nigerrima* Kröber, 1915 is treated as an unrecognised taxon (nomen dubium). Lectotypes are designated for *Physocephala pubescens* Brunetti 1925 and *P. curta* Kröber, 1936. *Physocephala kroeberi* (nom. nov.) is introduced for *Pseudophysocephala annulipes* Kröber, 1939, the latter being a junior secondary homonym of *Conops annulipes* Wiedemann in Meigen 1824. *Physocephala acroschista* (Speiser, 1911) is treated as valid species (status rev.). Diagnostic keys are presented for the Afrotropical *Physocephala* together with new faunistic records for 33 species.

**Key words.** Diptera, Conopidae, *Physocephala*, *Pseudophysocephala*, *Dacops*, new species, primary types, new synonyms, type species, lectotype designations, nomen dubium, nomen nov.m, status review, faunistic records, identification key.

## INTRODUCTION

This is the third and final part of a work presenting new faunistic records of the Diptera family Conopidae from the Afrotropical Region. The first part dealt with the subfamilies Myopinae and Stylogastrinae (Stuke 2015a), and the second part with all of the Conopinae except for the Physocephalini (Stuke in press). The present paper deals with the latter. As in the two previous papers, the original aim of the project was primarily to present new faunistic information, but this has necessitated extensive revisionary work in order to clarify the diagnosis of several of the species. As a result, new keys for all Afrotropical *Physocephala* species have had to be prepared, comprising a key to the nine species-groups currently recognised in the region as well as keys to the individual species in each group. The three publications together give a detailed overview of all of the valid Conopidae recognised in the

region at the present time, as well as summarising the known distribution.

## MATERIALS AND METHODS

As in the previous two parts of this series, the morphological terminology used in the species descriptions is mainly adopted from Cumming & Wood (2009). The terminology used to describe the postabdomen is additionally illustrated in Figs 5, 8 and 22–23. Since Kotrba (2000) concluded that sternite 9 is absent in the Cyclorhapha, the structure referred to as ‘syntergite 8+9’ in the previous papers is henceforward termed ‘tergite 8’ and the structure referred to as ‘sternite 9’ in the previous papers is henceforward termed ‘sternite 8’. The structures referred to as ‘sternite 8’ in the previous papers is not identified yet and henceforward termed ‘ventral sclerotisation’ (Londsdale, personal communication). The term



‘hair’ is discarded in favour of ‘setula’ since it is often impossible to distinguish between the two. Numbers of setae refer to one side of the body only. Any form of ‘microtomentosity’ is referred to by the more common term ‘dusting’.

The historically important collections held by MRAC, ZMHB and NHML were revisited and the material contained therein almost completely re-identified by JHS. In the NHML, however, there were many specimens held under ‘*Physocephala bimarginipennis*’ and ‘*Physocephala maculigera*’ which could not all be re-identified in detail due to time constraints.

Where new synonyms are introduced, the affected species names are given with the original combination in square brackets.

Faunistic records previously published elsewhere by JHS are not repeated here, other than where these require correction. Faunistic data is relayed from the specimen labels with as few changes as possible. A few locations have been altered to more commonly used names, and in a few cases provinces or an interpretation of the location have been added, all in square brackets. Locations which could not be found with an internet search, or abbreviations or characters which could not be resolved, are given in quotation marks. Coordinates are only included where these were present on the labels.

For primary type material, the labels are rendered as citations. The labels are listed and numbered in the order found, commencing with the uppermost. Line-breaks are indicated by a slash-mark [“ / ”] and where there are actual slash-marks on the labels themselves these are included without spaces before and after. Where text on labels could not be deciphered with certainty this is indicated by “[?]”. Persons mentioned on the labels of primary type material are given in small caps. Determination labels are also cited to assist in the interpretation of identifications given by previous researchers.

#### Abbreviations used for collections referred to in the text

- AMGS = Albany Museum, Grahamstown,  
South Africa, Cape Province
- BMSA = National Museum Bloemfontein,  
South Africa
- CAS = California Academy of Sciences,  
San Francisco, USA
- CULSP = Czech University of Life Sciences Prague,  
Czech Republic
- FMNH = Field Museum of Natural History, Chicago,  
USA
- IITA = International Institute of Tropical Agriculture,  
Abomey-Calavi, Benin
- ISNB = Institut Royal des Sciences Naturelles de  
Belgique, Brussels, Belgium

- MNHN = Muséum National d’Histoire Naturelle,  
Paris, France
- MRAC = Musée Royal de l’Afrique Centrale,  
Tervuren, Belgium
- MZLU = Lund University, Lund, Sweden
- NHML = The Natural History Museum of London  
[formerly the British Museum  
(Natural History) BMNH], London, UK
- NHRS = Naturhistoriska Riksmuseet,  
Stockholm, Sweden
- NMKE = National Museum of Kenya, Nairobi, Kenya
- PASS = priv. coll. Axel Ssymank (Germany, Bonn)
- PCFK = priv. coll. Christian F. Kassebeer  
(Germany, Damlos)
- PHJF = priv. coll. Hans-Joachim Flügel  
(Germany, Knüllwald)
- PJHS = priv. coll. Jens-H. Stuke (Germany, Leer)
- PMHA = priv. coll. Martin Hauser (USA, Sacramento)
- PMME = priv. coll. Maurizio Mei (Italy, Rome)
- RMNH = Nationaal Natuurhistorische Museum  
(“Naturalis”), Leiden, Netherlands
- SMNS = Staatliches Museum für Naturkunde,  
Stuttgart, Germany
- SMTD = Staatliches Museum für Tierkunde,  
Dresden, Germany
- SMWN = National Museum of Namibia,  
Windhoek, Namibia
- TAUI = Tel Aviv University, Tel Aviv, Israel
- UCDC = R.M. Bohart Museum of Entomology,  
University of California, USA
- USNM = Smithsonian Institution National Museum  
of Natural History [formerly the United States  
National Museum], Washington DC, USA
- ZFMK = Zoologische Forschungsmuseum Alexander  
Koenig, Bonn, Germany
- ZMHB = Museum für Naturkunde der  
Humboldt-Universität, Berlin, Germany
- ZSM = Zoologische Staatssammlung,  
München, Germany

Duplicates of newly designated type material are retained in the collection of JHS for further research.

The nomenclature used in this work is based on that given in the world checklist of Stuke (2017a), which listed all synonyms, type specimen depositories and representative faunistic records known at the time, together with relevant sources and literature references etc. Here-with we therefore include only new, additional or amended information on these matters where this is relevant to the Afrotropical Region.



## RESULTS

### CONOPINAE Macquart, 1834

The genera of Afrotropical Conopinae can be identified using the key of Stuke (in press).

### Physocephalini Smith & Peterson, 1987

To date three Afrotropical genera have been placed in the tribe Physocephalini, two of which (*Dacops*, *Pseudophysocephala*) are endemic or almost endemic to the region (Stuke 2016). The cladistic analysis of Gibson & Skevington (2013) concluded that Physocephalini is monophyletic, a position which has not been rejected since the tribe was introduced by Camras (1965) and subsequently defined by Smith & Peterson (1987).

Kröber (1939) differentiated the genus *Pseudophysocephala* only within a key, based on the characters “Kurze, gedrungene Arten mit grossem, flachem Kopf und mit lackartig glänzendem Einschnitt am Hinterrand des Auges” [short, stocky species with large, flat head and with shining depression at hind margin of eye]. The genus *Pseudophysocephala* was subsequently only referred to in publications by Camras (1962b, 2001), where he distinguished the genus using almost the same character set: “Head short (flat). Front, face, and cheek relatively narrow. Front usually not higher than eye. Indentation and triangle of eye large. Terminal female abdominal segments moderately to very aberrant.” Camras (1962b) stated that “By using the head characters, *Pseudophysocephala* has been maintained, although the intergradation of any one character is complete”. All of the diagnostic characters used by both Camras and Kröber are variable within both *Physocephala* and *Pseudophysocephala*, however, and although it is possible to recognise some distinct species-groups with obvious characters such as an aberrant theca or characteristic setae on tarsi, legs or pleura, none of the diagnostic characters mentioned by these two authors, nor any combination of these characters, is actually suitable to differentiate two genera. The type species of the genus *Pseudophysocephala*, *Conops platycephalus* Loew, 1853, is particularly intermediate and indeed very hard to identify at all. This difficulty has resulted in many problems in species identification given that the separation of *Physocephala* and *Pseudophysocephala* is the starting point in the recent keys of Camras (1962b, 2001). *Pseudophysocephala* and *Physocephala* fall together in the phylogenetic tree of Gibson & Skevington (2013). In their analysis, however, only two *Pseudophysocephala* species were included, both of which are treated in this paper as synonyms and neither of which reflects the huge morphological variability present within the genus. Only one character was mentioned by these authors to distinguish *Pseudophysocephala* and *Physo-*

*cephala*: [95-1] “Narrow female abdominal segments 5–7 present”. This character does not in fact distinguish the only species they used in their analysis from many *Physocephala* species, however, and is absent in several other *Pseudophysocephala* species. As a result, we here-with treat *Pseudophysocephala* Kröber, 1940 as a junior synonym of *Physocephala* Schiner, 1861 (**syn. nov.**).

Both of the known *Dacops* species are characterised by a single synapomorphy – ♀ postabdomen with a unique ventral spoon-shaped structure (Fig. 3) – and they are therefore without doubt sister species. No synapomorphic character has ever been found to show *Physocephala* to be monophyletic when excluding *Dacops*, however. Gibson & Skevington (2013) argued that *Physocephala* (including *Pseudophysocephala*) was monophyletic by virtue of one apomorphic character: [51-1] “metafemur distinctly broadened basally”. This character is suitable for diagnosing the tribe Physocephalini, but the slightly broadened hind femur of *Dacops* also falls within the variability found in this tribe. It may be that *Physocephala* without *Dacops* is paraphyletic, but no character has been found which consistently separates the two genera, and no taxonomic revision or phylogenetic study has so far considered enough species to cover the full range of variation. We therefore synonymise *Dacops* Speiser, 1923 with *Physocephala* Schiner, 1861 herewith (**syn. nov.**).

With the introduction of these new synonyms only the genus *Physocephala* remains in the Afrotropical Physocephalini. There are clearly distinct species-groups within this genus, as previously described by Camras (2001) and as indicated in Key 1, and it is possible that in future at least some of these will be found to be monophyletic, but probably not all. A full and detailed phylogenetic analysis which includes most of the Afrotropical species, and which follows the important comments made by Borkent (2018: 113), will be necessary in the future in order to fully clarify the position and, where necessary, allow the rational division of *Physocephala* into well-supported genera and/or subgenera.

### *Physocephala* Schiner, 1861

- = *Pseudodacus* Kröber 1915, homonym of *Pseudodacus* Hendel, 1914 [Tephritidae]
- = *Dacops* Speiser, 1923 (**syn. nov.**)
- = *Archiphysocephala* Kröber, 1939 [Camras 1957, Smith & Cunningham-van Someren 1970]
- = *Pseudophysocephala* Kröber, 1940 (**syn. nov.**)

Although *Physocephala* species are among some of the most conspicuous and beautiful Conopidae the identification of species is very difficult due to high infraspecific variation and the lack of stable characters to divide the genus in groups. Key 1 presents a new attempt to distinguish species-groups but we are very aware that this re-



mains problematic. In many cases it will not be possible to identify single specimens of difficult species without comparative material. Much patience is necessary, and no little frustration encountered, when identifying Afrotropical *Physocephala*!

It should be noted that the species-groups given below are not intended to represent natural monophyletic groupings but are merely an attempt to provide a starting point for the identification of species within this large genus. Where our species-groups are identical to those previously identified by Camras (2001) we have retained the same species-group name, but where they are constituted or interpreted differently we have used a different name in order to minimise confusion in the future.

### Key 1 – Identification of Afrotropical *Physocephala* species-groups

1. Mediotergite with distinct setae (e.g. Fig. 148); tibiae may have black setulae arranged to form a dorsal line (e.g. Fig. 140); vertex occupying almost half length of frons (except in *brevivertex*); semi-circular, setose and may have distinct ocellar scar (e.g. Figs 129, 131); apical aristomere may be extremely long in some species, twice as long as first aristomere including ventral projection (e.g. Figs 132, 149); wing completely covered with microtrichia; cell  $r_{2+3}$ , basal cell and basal medial cell completely dark brown to black (e.g. Fig. 142); facial carina medially black to brown..... ***P. pubescens* species-group**
- Mediotergite at most with some barely visible short setae; tibiae lack black setulae arranged in dorsal lines; vertex clearly shorter than half length of frons; other characters variable (e.g. Fig. 15); apical aristomere never extremely long, much less than twice length of first aristomere including ventral projection; wing in some species with areas lacking microtrichia; wing less darkened in some species; facial carina completely yellow in some species .... **2**
2. Knob of haltere at least partly velvety black (e.g. Fig. 67); arista three-segmented (e.g. Fig. 39); pleura lacks vertical dusting stripe..... **3**
- Knob of haltere at most with some obscure darkening but never velvety black; arista with two or three distinct aristomeres; pleura may have vertical dusting stripe (e.g. Fig. 25) ..... **4**
3. Frontoclypeal tubercle larger than adjoining lateral facial groove, dorsally rounded and lacking keel (Fig. 37); hind margin of eye lacks a shining triangular indentation; scape shorter, about 2.5 times as long as high, apical aristomere as shown in Fig. 39; vertex short, and with longitudinal grooves (Fig. 38); wing as in Fig. 41: basal cell and basal medial cell completely brown and covered

with microtrichia; vena spuria starts in middle of crossvein  $rm$  and reaches the hind margin of cell  $r_{4+5}$ , therefore separating off a narrow triangular area; ♂ with distinctly pointed tip to abdomen in side view (Fig. 40); larger species, abdomen not so obviously narrow and elongated (Fig. 40); wing length 15–20 mm..... ***P. bimarginipennis* species-group**

- Frontoclypeal tubercle smaller than adjoining lateral facial groove, dorsally with sharp keel (e.g. Fig. 66); hind margin of eye has distinct shining triangular indentation (e.g. Fig. 80); scape long, about four times as long as broad (e.g. Fig. 66), apical aristomere elongated; vertex not obviously short and at most with a few longitudinal grooves; wing as e.g. Fig. 70: basal cell and basal medial cell partly hyaline and partly without microtrichia; vena spuria starts close to hind margin of cell  $r_{4+5}$ , therefore not separating off any distinct area; ♂ abdomen with rounded tip in side view (i.e. lacking distinct point; e.g. Fig. 67); smaller species with very narrow and elongated abdomen reaching well beyond wing tips (e.g. Fig. 67); wing length 7–10 mm ..... ***P. halterata* species-group**

4. Vena spuria in cell  $r_{4+5}$  usually well developed, starting in anterior half of radial-medial crossvein and therefore distinctly separated from media at least in basal  $\frac{1}{3}$  of cell  $r_{4+5}$  (e.g. Fig. 118). In occasional specimens where the radial-medial crossvein is reduced, this character may not be distinct; cell  $r_{4+5}$  hyaline between media and vena spuria (e.g. Fig. 118, 122) and sometimes lacking microtrichia there; dark species lacking distinct colour pattern (e.g. Fig. 108, 122); scutum and scutellum black to brown, tergites 1–3 dark brown to reddish-brown, tergites 3–6 black to dark brown (except in *P. rufa*, which is principally reddish-brown); abdomen lacks obvious dense dusting, only tergite 3 may have posterolateral silver-grey dusted spots (e.g. Fig. 108, 122); anterior part of abdomen obviously narrow and elongated (e.g. Fig. 122); hind margin of eye with distinct shining triangular indentation, and occiput obviously bulging forward at this point; scape elongated, at least as long as protruding part of face; gena very narrow, not broader than maximum width of proboscis; frons with darker black or brown mark, or indistinct light brown marking; mediotergite usually has some barely visible short setae; ♀ fore tarsi sometimes obviously broad and/or with unusual structures such as long setae (e.g. Fig. 114) or long and narrow or spine-like pulvilli (e.g. Fig. 120); hind tarsi sometimes extremely short (e.g. Fig. 111); ♀ theca reduced, aberrant and not protruding far ventrally (e.g. Figs 110, 115, 124); ♂ sternite 5 sometimes v-shaped or u-shaped posteriorly ..... ***P. pilitarsis* species-group**



- Characters never in the above combination; vena spuria in cell  $r_{4+5}$  sometimes indistinct or missing (e.g. Fig. 100); cell  $r_{4+5}$  sometimes completely brown between media and vena spuria, if vena spuria is developed at all; several species are paler and have a distinct colour pattern, e.g. orange scutum with black markings; abdomen usually with obvious dusting, tergites 3–4 with densely dusted hind margin and at least tergites 5–6 with obvious golden dusting; anterior part of abdomen sometimes wider and shorter (e.g. Fig. 57); if hind margin of eye has a distinct shining triangular indentation, then occiput usually less obviously bulging forward at this point; scape sometimes shorter than protruding part of face; gena sometimes wider than maximum width of proboscis; frons may lack dark marking; mediotergite lacks any short setae in several species; ♀ tarsi lacking unusual characters; ♀ theca in almost all species normally developed and obviously protruding ventrally; ♂ sternite 5 straight-edged or only slightly concave posteriorly ..... **5**
- 5.** ♀ postabdomen ventrally with unique protruding spoon-shaped structure (e.g. Fig. 3), theca absent; ♂ abdomen slightly pointed in side view (e.g. Fig. 2); epandrium long, small cerci reaching only about 1/4 of the length of epandrium (e.g. Fig. 4); hypandrium sheath narrow and elongated; distiphallus elongated and aedeagus may therefore be obviously extruded (e.g. Fig. 5); cell  $r_{2+3}$  only dark in apical half (e.g. Fig. 1) or cell  $r_{4+5}$  completely dark (e.g. Fig. 6) ..... ***P. abdominalis* species-group**
- ♀ postabdomen ventrally lacks protruding spoon-shaped structure, but has theca; ♂ abdomen not pointed in side view but rounded (e.g. Fig. 66, 71); epandrium smaller and therefore cerci reaching more than 1/4 of the length of epandrium; hypandrium sheath different (as far as is known) and distiphallus less elongated; wing pattern may be different, or same as above ..... **6**
- 6.** Arista extremely short, appearing as if broken (e.g. Figs 16, 32); aristomeres all shorter than height of basal aristomere; in most species only two visible aristomeres; scape in most species shorter, about twice as long as high (e.g. Fig. 13); shining triangular area at hind margin of eye barely developed or absent; vertex anteriorly with more or less distinct longitudinal groove (e.g. Fig. 15); radial-medial crossvein usually not obviously short and never completely reduced (e.g. Figs 12, 20, 21); basal cell may be partially bare of microtrichia (e.g. Figs 9, 10); anepimeron may have setulae; ♂ sternite 8 slightly to distinctly bulging over protandrium; typically with very fine black setulae (distinctly smaller than the scattered setulae on protandrium) arranged in distinct line at border between protandrium and sternite 8; ♂ epandrium as e.g. Figs 7–8, 22–23: blackish teeth on posterior margin of epandrium with more or less broad blackened bases; epandrium with long setulae anteromedially and dorsally; in lateral view large apically and almost semi-circular; postgonite evagination on inner side with broad-based spines giving this structure a fish-scaled appearance (may be hard to see in strongly macerated specimens, character not proven in all species); ♀ postabdomen lacking obvious reductions or aberrant theca (e.g. Fig. 14, 19), tergite 6 always large and elongated (e.g. Fig. 19) ..... **7**
- Arista usually longer and v-shaped (e.g. Figs 48, 65), both aristomeres distinctly longer than high; scape sometimes more than twice as long as high (e.g. Figs 47, 66); distinct shining triangular area at hind margin of eye (e.g. Figs 72, 80); vertex lacks anterior longitudinal groove in some species (e.g. Figs 84, 85, 87); radial-medial crossvein sometimes very short or absent (e.g. Fig. 100); basal cell completely covered with microtrichia; anepimeron lacks setulae; ♂ shining sternite 8 not usually bulging over protandrium; border between protandrium and sternite 8 usually lacks line of fine black setulae; ♂ epandrium sometimes different to above (but is unknown in some species); ♀ postabdomen may have obvious reductions or an aberrant theca, tergite 6 sometimes very small (e.g. Fig. 55) ..... **8**
- 7.** Hind coxa not dusted, or at least not more densely dusted than middle and fore coxae; pleura usually lacks dense dusting; if dusting stripe is present it starts at a point clearly separated from middle coxa and becomes narrower before reaching notopleuron; typically, mediotergite dorsally lacks dense dusting connecting with dense dusted spot on katatergite; costal cell and subcostal cell always hyaline, obviously paler than base of cell  $r_{2+3}$ , cell  $r_{2+3}$  typically hyaline distally, with isolated spot around vein  $R_{4+5}+M_1$  ..... ***P. vittata* species-group**
- Hind coxa more densely dusted than middle and fore coxae (e.g. Fig. 14); pleura usually with dusting stripe running vertically from middle coxa and often reaching notopleuron without narrowing; typically, mediotergite dorsally with dense dusting connecting with dense dusted spot on katatergite; wing with different colour pattern ..... ***P. antiqua* species-group**
- 8.** Ventral projection of basal aristomere towers over apical aristomere (e.g. Figs 48, 50, 58); radial-medial crossvein always distinct; vena spuria in cell  $r_{4+5}$  distinct, starting at radius  $R_{4+5}$  and usually fused with or closely approximated to media; wing membrane between vena spuria and media hyaline (e.g. Fig. 49); scutum usually with two sublateral dusting stripes



starting at inner side of postpronotum and fused before scutellum (e.g. Fig. 42); ♀ theca normally developed but usually depressed towards or against the abdomen (i.e. not projecting perpendicularly, e.g. Fig. 54); ♀ abdomen obviously short, tergites 5 and 6 much shorter than tergite 4 (e.g. Figs 55, 57) .....

.....***P. caenoneura* species-group**

- Apical aristomere usually longer than ventral projection of basal aristomere (e.g. Fig. 79); radial-medial crossvein sometimes reduced or absent (e.g. Fig. 100); vena spuria in cell  $r_{4+5}$  absent, or if developed then membrane between vena spuria and media not hyaline (e.g. Fig. 83); scutum may lack sublateral dusting stripes; ♀ theca sometimes very reduced, or projects more perpendicularly from abdomen (e.g. Fig. 77, 102); ♀ abdomen may be short or long .....***P. microvena* species-group**

### ***Physocephala abdominalis* species-group**

Species of the *Physocephala abdominalis* group were previously placed in the genus *Dacops*. Females are easily recognised by the unique spoon-shaped structure which projects ventrally at the apex of the abdomen, and the lack of any theca (Figs 2, 3). The precise morphological derivation of the spoon-shaped structure is not obvious to us, and does not appear to have been established elsewhere, but given the scarcity of the available material we have not carried out any dissections as the structure is clearly visible without. Males are much more difficult to diagnose because all of the characters used in Key 1 are variable, and atypical forms occur. Males of *Physocephala kaplanae* may occasionally have a reduced radial-medial crossvein and barely developed vena spuria, making them easy to misidentify as a member of the *microvena* group, although the characteristic male postabdomen shape, as described in Key 1, should nevertheless allow these to be safely assigned. All members of the *abdominalis* species-group are confined to the Afro-tropical Region.

### **Key 2 – Identification of the *Physocephala abdominalis* species-group**

1. Basal cell completely hyaline and not covered with microtrichia (Fig. 1); wing between costa and radius  $R_{2+3}$  hyaline (Fig. 1); black colouration on scutum not reaching hind margin; overall appearance reddish-brown, but may sometimes be brownish to blackish  
***P. abdominalis* (Kröber, 1915)**
- Basal cell completely or almost completely dark, and completely covered with microtrichia (Fig. 6); wing between costa and radius  $R_{2+3}$  dark (Fig. 6); black colouration on scutum may reach to hind margin; overall appearance black ..... ***P. kaplanae* (Camras, 2001)**

### ***P. abdominalis* (Kröber, 1915)**

(Figs 1–5)

*Pseudodacus abdominalis* Kröber 1915

= *Pseudodacus apicalis* Kröber, 1915

= *Physocephala fascipennis* Brunetti, 1925

= *Conops patelliformis* Séguy, 1933

**Primary type material examined.** 1♂ syntype of *Physocephala fascipennis* Brunetti, 1925: (1) “Syn - / type”; (2) “12.II.11 / Caia / Zambesi / Dhawar / H. Swale.”; (3) “Pres. by / Impl. Bureau Ent. / 1915 - 164”; (4) “*Physo. / fascipennis* / Brun. Type ♂ / Det. E. Brunetti 1924”; (5) “BMNH(E)# / 249047”; coll. NHML.

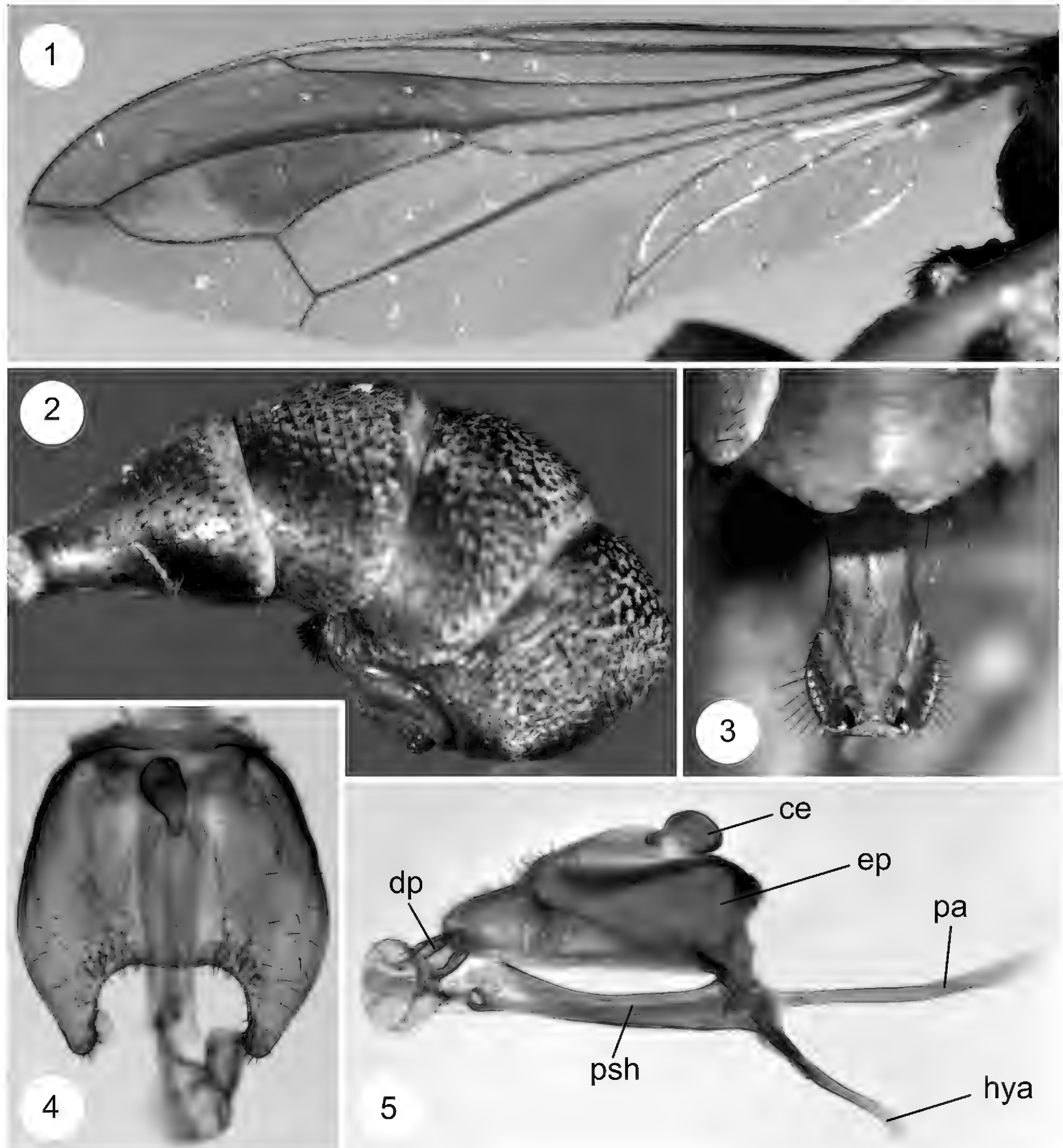
1♀ syntype of *Physocephala fascipennis* Brunetti, 1925: (1) “Syn - / type”; (2) “Nyasaland / Cholo / R. C. Wood”; (3) “Pres. by / Imp. Bur. Ent. / Brit. Mus. / 1924 - 306”; (4) “*Physo. / fascipennis* / Brun. Type ♀ / Det. E. Brunetti 1924”; (5) “BMNH(E)# / 249048”; coll. NHML.

**Additional material.** BENIN: 1♀, vi.2002, Pénésoulou, forest area [09°15'58.26"N 01°33'04.81"E], leg. G. Goergen, coll. IITA; 1♂, 28.i.2018, Togbota, leg. G. Goergen, coll. IITA; DEMOCRATIC REPUBLIC OF CONGO: 1♂, iv.1913, Congo da Lemba, det. as *P. fascipennis* by Brunetti 1925, leg. R. Mayné, coll. MRAC; 1♂, 1942, Bas-Congo, Mayidi, leg. P. Van Eyen, coll. ISNB; 1♀, 1945, ditto; ETHIOPIA: 1♀, iii.1969, Bahir Dar, leg. Schäuuffele, coll. SMNS; 2♂♂, 30.–31.v.2015, Sof Umer [6°54'N 40°51'E], 1200 m, leg. J. Halada, coll. CULSP; KENYA: 1♂, xi.1948, Garissa-Bura, Tana River, det. as *D. abdominalis* by Camras 1999, leg. van Someren, coll. NHML [NHMUK010922084]; 1♂, 12.x.1998, Morigat, leg. F. Kaplan, A. Freidberg, coll. TAUI; 1♀, 12.–26.ii.2005, Nyanza Province, Ungoye Field Station [0°36.91'S 34°05.52'E], 1147 m, leg. R. Copeland, coll. NMKE; MALAWI: 1♂, 11.v.1916, Nyasaland, Ruvo Valley, 1000–2000 ft, des. as syntype of *P. fascipennis*, leg. R. C. Wood, coll. NHML [NHMUK010922076]; MOZAMBIQUE: 1♀, 19.–30.iv.2015, Sofala pr., Gorongosa Park, small lake [18°56'39"E 34°26'35"E], 30 m, Malaise trap, leg. M. Hauser, A. Rung, coll. PMHA; SOUTH AFRICA: 1♂, i.2000, Mondl Forest, Hilton, KZN, leg. Lyawb, coll. PMHA; 1 specimen, i.–iii.1927, Natal, Weenen, det. as *D. abdominalis* by Kröber 1930, leg. H. P. Thommaset, coll. NHML [NHMUK010922090]; 1♀, xii.1923, Natal, Weenen, det. as *D. fascipennis* by Brunetti 1924, leg. H. P. Thommaset, coll. NHML [NHMUK010922093]; 1 specimen, 2.x.1915, Umbilo, Durban, Natal, des. as syntype of *P. fascipennis*, [collector unknown], coll. NHML [NHMUK010922077]; 1♂, iv.1955, Cape Province, Grahamstown, det. as *D. fascipennis* by Smith 1957, leg. Allison, coll. NHML [NHMUK010922088]; 1♂, 26.xi.1958, Cape Province, Grahamstown, leg. C. Jacot-Guillarmod, coll. AMGS; 1♂, 2.xii.1958, ditto; 1♀, 17.xi.1961, Cape Province, Grahamstown, leg. E. McC Callan, coll. AMGS; 1♂,



19.xii.1971, Cape Province, Grahamstown, det. as *D. abdominalis* by Camras 2000, leg. D. J. Greathead, coll. NHML [NHMUK010922085]; 1♀, 26.ii.1987, Cape Province, Grahamstown, leg. P. E. Hulley, coll. AMGS; 1♂, 7.vii.2002, Cape Province, Grahamstown [33.17°S 26.31°E], leg. H. V. Lewis, coll. AMGS; 1♀, 15.ix.2006,

Cape Province, Grahamstown [33°23'S 26°29'E], leg. A. McClure, coll. AMGS; 1♂, 4.iv.1981, Cape Province, Grahamstown [33°19'S 26°31'E], leg. G. T. Lloyd, coll. AMGS; 1♀, 10.iii.1981, Cape Province, Grahamstown, 200 Dept. window [33.19S 26.32E], leg. E. Nieman, coll. AMGS; 2♂♂, 22.i.1970, Cape Province, Grahamstown,



**Figs 1–5.** *Physocephala abdominalis* (Kröber, 1915). 1. Wing, dorsal view (♂, Belmont Valley); 2. Tip of ♂ abdomen, lateral view (♂, Belmont Valley); 3. Spoon-shaped structure of ♀ postabdomen (♀, Zambesi Valley); 4. Epandrium, dorsal view (♂, Grahamstown); 5. Postabdomen, lateral view (♂, Grahamstown). ce = cercus; dp = distiphallus; ep = epandrium; pa = phallapodeme; hya = hypandrial arm; psh – phallus sheath.



Belmont Valley, on flowering *Foeniculum vulgare* Mill., leg. F. W. Gess, coll. AMGS; 2♂♂, 23.i.1970, Cape Province, Grahamstown, Belmont Valley, on flowering *Foeniculum vulgare* Mill., leg. F. W. Gess, coll. AMGS; 2♂♂, 26.i.1970, Cape Province, Grahamstown, Belmont Valley, on flowering *Foeniculum vulgare* Mill., leg. F. W. Gess, coll. AMGS; 1♂ 1♀, 25.i.1972, Cape Province, Grahamstown, Belmont Valley, leg. F. W. Gess, coll. AMGS; 1♂, 6.i.1977, Cape Province, Grahamstown, Hilton [-33.310629 26.525595], on *Acacia karroo* flowers, leg. D. W. Gees, coll. AMGS; 1♂, 2.xii.1979, Cape Province, Grahamstown, Hilton [-33.310629 26.525595], leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 6.–14.i.1972, Cape Province, Grahamstown, Howison's l'oort, leg. F. W. Gess, coll. AMGS; 1♀, 19.–22.xi.1971, ditto; 1♂, 8.–9.iv.1979, Cape Province, Salt Vlei, Port Alfred, leg. A. E. Mel. Collan, coll. AMGS; 1♂, 19.xi.1999, Eastern Cape Province, 37 km nw of Steytlerville [33°11'S 24°10'E], 695 m, leg. M. Hauser, coll. PMHA; 1♂, 1.–10.ii.1933, Eastern Cape Province, Katberg, det. as *D. abdominalis* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922087]; 1♂, 1.–10.ii.1933, Eastern Cape Province, Katberg, det. as *D. abdominalis* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922089]; 1♀, 1.–10.ii.1933, Eastern Cape Province, Katberg, det. as *D. abdominalis* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922092]; 1♀, 1.–10.ii.1933, Eastern Cape Province, Katberg, det. as *D. abdominalis* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922094]; 1♂, 1.–10.ii.1933, Eastern Cape Province, Katberg, det. as *P. platycephala* by Kröber, 1938, det. as *P. rufitarsis* by Camras 2000, leg. R. E. Turner, coll. NHML [NHMUK010922157]; 1♂, 26.ix.2010, Free State Province, Bloemfontein, 10 Jan Venter Street [29°06'12"S 26°08'42"E], leg. R. J. Nuttall, coll. BMSA; 1♀, 26.ix.2010, Free State Province, Bloemfontein, 10 Jan Venter Street [29°06'12"S 26°08'42"E], on window, leg. R. J. Nuttall, coll. BMSA; 1♂, xii.2009, Free State Province, Bloemfontein, Nation-

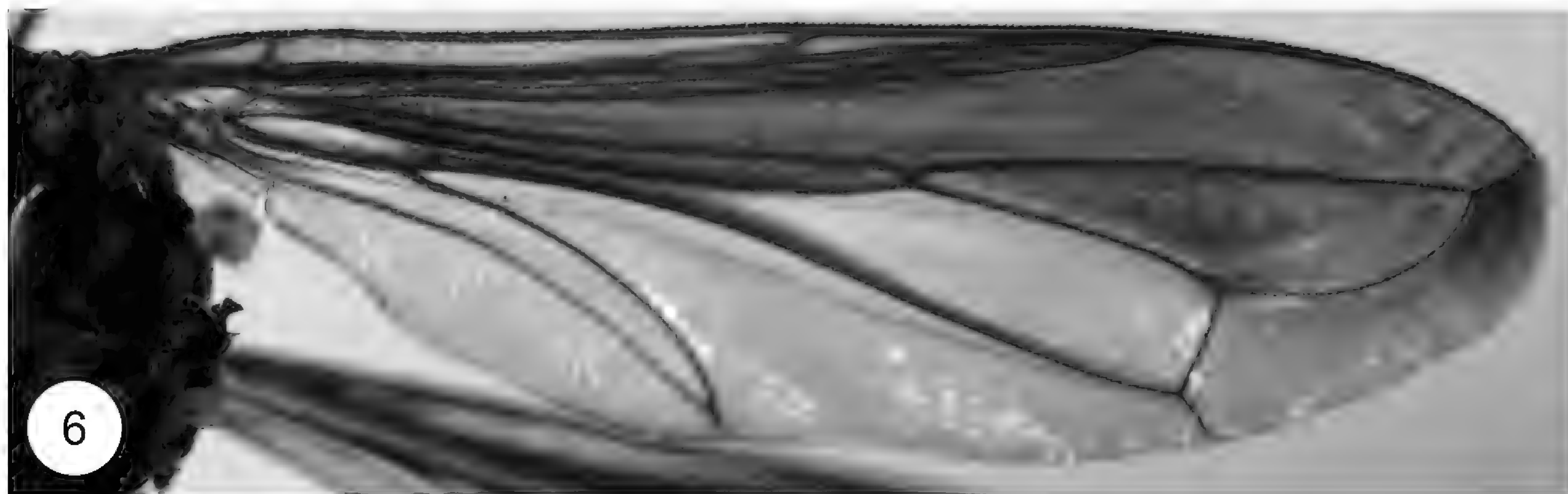
al Museum Library [29°6'54.35"S 26°13'9.72"E], leg. L. Coetzee, coll. BMSA; 1♀, 13.xii.2012, KwaZulu-Natal Province, Pietermaritzburg, Kwela Lodge, 940 m, leg. B. Lechner, coll. PASS; 1♂, 22.–25.xi.2003, Mpumalanga Province, 30 km ne Lydenbrug near Ohrig, leg. J. Halada, coll. CULSP; 1♀, no date, Natal Province, Howick, des. as syntype of *P. fascipennis*, leg. J. P. Gregor, coll. NHML [NHMUK010922078]; 1♂, 14.i.1953, Natal Province, St. Michael, det. as *D. fascipennis* by Smith 1957, on flowers of *Scutia myrtina*, leg. E. McC Callan, coll. NHML [NHMUK010922086]; 1♂, 28.iv.2002, Western Cape Province, Nature Valley, 33 23 DC, leg. L. de Wet, coll. AMGS; TANZANIA: 1♂, 10.v.1956, Old Shinyanga, Block 9, det. as *P. caenoneura* by Emden 1950, leg. E. Burt, coll. NHML [NHMUK010922143]; ZIMBABWE: 1♀, 13.iii.1936, Salisbury [= Harare] [17.84 31.05], leg. W. L. Williams, coll. NHML [NHMUK010922091]; 1♂, 24.vii.1958, Salisbury [= Harare] [17.84 31.05], leg. A. D. Graham, coll. AMGS; 1♀, ii.1987, Zambesi Valley, Rekometjie [16°10'S 29°25'E], leg. S. Gußmann, coll. ZFMK; UNKNOWN LOCATION: 1♀, 27.xii.1937, [characters illegible], det. as *D. abdominalis* by Kröber 1938, leg. A. I. Bevis, coll. NHML [NHMUK010922095].

***P. kaplanae* (Camras, 2001)**

(Fig. 6)

*Dacops kaplanae* Camras 2001

**Material.** CENTRAL AFRICAN REPUBLIC: 1♀, 17.xii.2008, 45 km e Nola [03°40'N 16°26'E], 570 m, leg. J. Halada, coll. CULSP; DEMOCRATIC REPUBLIC OF CONGO: 1♂, 1968, Tshuapa, Bamanya, leg. P. Hulstaert, coll. MRAC; ETHIOPIA: 1♀, 4.xi.2018, Bahir Dar [11.597292°N 37.355696°E], leg. G. Goergen, coll. IITA; 1♀, 11.xii.2014, Bonga, Straßensaum, 1955 m [07°14'09"N 036°16'36"E], leg. H.-J. Flügel, coll. PHJF; 1♂, 20.ix.2012, Chench, 1916 m [06°09'N 37°34'E], leg. A. Pauly, coll. ISNB; 1♂, 1912, Harar, leg. S. V. Kris-



**Fig. 6.** *Physocephala abdominalis* (Kröber, 1915). 1. Wing, dorsal view (♂, Belmont Valley); 2. Tip of ♂ abdomen, lateral view (♂, Belmont Valley). Wing of *Physocephala kaplanae* (Camras, 2001), dorsal view (Monts de Christal).



tensen, coll. ZMHB; 1♀, 18.x.1957, near Axum, paratype of *P. kaplanae*, det. as *D. abdominalis* by Smith 1969, leg. D. J. Greathead, coll. NHML [NHMUK010922075]; GABON: 1♂, 11.–12.iii.1990, Wolen-Ntem, Monts de Christal, Tchimbélé, 600 m [00°37'N 10°24'E], leg. J. J. Wieringa, coll. RMNH.

It is possible that *P. kaplanae* is nothing more than a darker form of *P. abdominalis*, although we are not aware of any intermediates and therefore accept the validity of this species.

### *Physocephala antiqua* species-group

All of those species which Camras (2001) placed in his *maculipes* and *similis* species-groups are herewith included within the *antiqua* species-group. The segregation of the Camras species-groups is difficult or impossible due to the extreme variability of the characters used to separate them, and it is therefore more convenient to combine them. In general, members of the *antiqua* species-group have a very typical *Physocephala* habitus lacking any atypical characters other than an extremely short arista. Careful evaluation of the character combination set out in Key 1 is necessary to distinguish members of this group, however, especially males. Several species of this group are restricted to the Afrotropical Region but others have a wider distribution which reaches into southern and central Europe, with some also reaching eastwards as far as China and Mongolia. The species-group also contains several Palearctic species which are not currently known from the Afrotropical Region.

### Key 3 – Identification of the *Physocephala antiqua* species-group.

1. Basal cell completely covered with microtrichia, and usually brownish in colouration ..... 2
  - Basal cell almost completely (or at least centrally) bare of microtrichia and hyaline ..... 4
2. Wings obviously reduced in length, not reaching beyond apex of tergite 3 (Fig. 11) ..... *P. brevipennis* Camras, 1962
  - Wing not obviously reduced, about as long as abdomen or at least extending beyond apex of tergite 3 ..... 3
3. Cell  $r_{2+3}$  completely brown (Fig. 21); subcosta light yellow to yellowish-brown, obviously different in colour from radial veins (Fig. 21); legs orange-brown, lacking a blackish ring on hind femur or darkened tarsi (Fig. 14); scutum orange-brown with black central stripe and small two lateral black spots which may sometimes fuse with mid-stripe (Fig. 17);

scutellum orange-brown (Fig. 17); larger species, wing length 6.3–7.6 mm.... *P. guillarmodi* spec. nov.

- Cell  $r_{2+3}$  hyaline apically (Fig. 36); subcosta dark brown, same as radial veins (Fig. 36); at least hind femur with black markings, and apical tarsi black; scutum and scutellum sometimes blackish; smaller species, wing length 3.7–5.3 mm (based on 3 known Afrotropical specimens only) ..... *P. pusilla* (Meigen, 1804)

4. Anepimeron with long setulae, about as long as maximum width of tibiae; dusting stripe on pleura distinct, narrow at anepisternum and broader when reaching notopleuron (Fig. 34), obviously contrasting with shining anterior half of anepisternum and anepimeron (Fig. 34) ..... *P. ssymanki* spec. nov.
  - Anepimeron at most with short setulae; any dusting stripe on pleura reaching notopleuron without widening, and sometimes indistinct ..... 5
5. 3 aristomeres, the basal one minute and easily overlooked; scape usually about three times as long as high (Fig. 28); gena black, and parafacia above gena mainly yellow (Fig. 28); frons with black longitudinal stripe reaching from vertex to base of antennae (Fig. 26); black facial stripe divided ventrally and reaching to mouth edge (Fig. 28); abdomen longer (Fig. 25), ratio of combined dorsal length of tergites 2+3 : dorsal length of tergite 4 in ♂ > 3.8 ..... *P. larvata* (Speiser, 1911)
  - 2 aristomeres (e.g. Fig. 28); scape usually only about twice as long as high; gena and frons lack black markings; abdomen shorter, ratio of combined dorsal length of tergites 2+3 : dorsal length of tergite 4 in ♂ < 3.5 ..... 6
6. Wing completely hyaline (Fig. 12) ..... *P. claripennis* Becker, 1923
  - Wing with distinct brown to blackish markings (Figs 9, 10) ..... *P. antiqua* (Wiedemann, 1830)

### *P. antiqua* (Wiedemann, 1830)

(Figs 7–10)

*Conops antiqua* Wiedemann 1830

= *Conops maculipes* Bigot, 1887 **syn. nov.**

= *Conops interrupta* Bezzi, 1901

= *Conops erythrasis* Bezzi, 1901

= *Physocephala flavifacies* Kröber, 1915

= *Physocephala limbata* Kröber, 1915

= *Physocephala rubicunda* Kröber, 1915

= *Physocephala madagascariensis* Kröber, 1915 **syn. nov.**

= *Physocephala gracilia* Kröber, 1915 **syn. nov.**

= *Physocephala decisa* Brunetti, 1925

= *Physocephala brevistylata* Kröber, 1931

= *Physocephala minutissima* Kröber, 1933 **syn. nov.**

= *Physocephala nigroscutellata* Kröber, 1933



**Primary type material examined.** ♀ holotype of *Conops maculipes* Bigot, 1887: (1) “Holo - / type”; (2) “S. Africa: / Cape of Good Hope. / ex coll. J. Bigot / ex coll. G. H. Verrall / B.M. 1914-500 [strikethrough]”; (3) “*C. maculigera* ♀ / Cap. B. Hop.”; coll. NHML.

♂ holotype of *Physocephala rubicunda* Kröber, 1915: (1) “3055”; (2) “Type”; (3) “*Physocephala* ♂ / *rubicunda* Krb. / O. Kröber det. 1914”; coll. ZMHB.

♂ syntype of *Physocephala decisa* Brunetti 1925: (1) “Syn- / type”; (2) “N. E. Rhodesia. / Upper Luangwa R. / 27 July 13 Aug. 1910. / S. A. Neave”; (3) “*Physocephala* / *decisa* / Brun. Type ♂ / Det. E. Brunetti 1924”; (4) “BMNH(E)# / 249074”; coll. NHML.

♀ syntype of *Physocephala decisa* Brunetti 1925: (1) “Syn- / type”; (2) “N. E. Rhodesia. / Upper Luangwa R. / 27 July 13 Aug. 1910. / S. A. Neave”; (3) “*Physocephala* / *decisa* / Brun. Type ♀ / Det. E. Brunetti 1924”; (4) “BMNH(E)# / 249077”; coll. NHML.

♀ syntype of *Physocephala decisa* Brunetti 1925: (1) “Syn- / type”; (2) “Rusapi / S. Rhodesia / 19.12.1920 / Rhodesi / Museum”; (3) “Pres. by. / Imp. Bur. Ent. / Brit. Mus. / 1924-306”; (4) “*Physocephala* / *decisa* / Brun. / Type ♀ / Det. E. Brunetti 1924”; (5) “BMNH(E)# / 249075”; coll. NHML.

♂ holotype of *Physocephala minutissima* Kröber, 1933: (1) “1” “Holo- / type”; (2) “Type”; (3) “8.6.16 / Ruo / Nyasaland / 200 ft / R. C. Wood / 601.”; (4) “Pres. by. / Imp. Inst. Ent. / Brit. Mus. / 1931-480”; (5) “*Physocephala* / *minutissima* / ♂ Krb”; (6) “BMNH(E)# / 249071”; coll. NHML.

♀ holotype of *Physocephala nigroscutellata* Kröber 1933: (1) “Holo- / type”; (2) “Type”; (3) “Lady Grey / 1 Feb. 1924 / R. I. Nel”; (4) “Pres. by / Imp. Inst. Ent. / Brit. Mus. / 1932-143.”; (5) “*Phsocephala* / *nigroscutella* [sic] / ♀ Krb / det. Kröber 1931”; (6) “BMNH(E)# / 249072”; coll. NHML.

**Additional material.** BENIN: 1♀, ix.2006, Adohoun [06°39'27.55"N 01°39'09.76"E], light trap, leg. G. Goergen, coll. IITA; 1♂, v.2007, Athiémé [06°14'20.00"N 01°40'00.00"E], leg. G. Goergen, coll. IITA; 1♂, viii.2006, Athiémé [06°14'20.00"N 01°40'00.00"E], sweep netting, leg. G. Goergen, coll. IITA; 1♀, 14. vi.2006, Calavi, sweep netting, leg. G. Goergen, coll. IITA; 1♂, 7.viii.2006, Calavi, campus [06°26'15.00"N 02°19'42.00"E], sweep netting, leg. G. Goergen, coll. IITA; 1♀, 25.x.2007, ditto; BURUNDI: 1♀, 24.viii.1957, Kisenyi, leg. F. J. François, coll. ISNB; 1♀, 22.i.1950, Rumonge, 780 m, det. as *P. nigroscutellata* by Janssen 1954, leg. F. J. François, coll. ISNB; 1♂, 9.iii.1952, Bubanza Province, 7 km s de Gihanga, 850 m, det. as *P. nigroscutellata* by Janssen 1954, leg. F. J. François, coll. BMSA; CAMEROON: 1♀, 24.iv.1914, Uamgebiet, Bossum, leg. G. Tessmann, coll. ZMHB; 1♀, 12.v.1914, Uamgebiet, Bossum, det. as *P. interrupta* by Kröber, leg. G. Tessmann, coll. ZMHB; CENTRAL AFRICAN RE-

PUBLIC: 1♀, 14.v.2009, 45 km ssw Bamingui [07°15'N 20°03'E], leg. J. Halada, coll. CULSP; 1♂, 20.iv.2010, Reserve Koukorou Bamingui [07°15'N 20°03'E], 440 m, leg. J. Halada, coll. CULSP; DEMOCRATIC REPUBLIC OF CONGO: 1♀, i.-ii.1913, Congo da Lemba, det. as *P. decisa* by Brunetti 1925, leg. R. Mayné, coll. MRAC; ETHIOPIA: 1♂, 24.v.2015, 10 km nw Mega [04°08'N 38°16'E], 1670 m, leg. J. Halada, coll. CULSP; 8♂♂, 11.-13.v.2015, 20 km se Konsa [05°15'N 37°32'E], 850 m, leg. J. Halada, coll. CULSP; 1♂ 2♀♀, 14.v.2015, 40 km w Konso [5°19'N 37°04'E], 600 m, leg. J. Halada, coll. CULSP; 1♂, 10.v.2015, 45 km ne Arba Minch [6°17'N 37°47'E], 1200 m, leg. J. Halada, coll. CULSP; 1♀, 21.iv.2016, Arsi [7°49'06"N 40°31'52"E], 886 m, leg. J. Halada, coll. CULSP; 1♀, 22.v.2015, Wachile env. [04°32'N 39°03'E], 1070 m, leg. J. Halada, coll. CULSP; GAMBIA: 1♂, 4.xi.1977, Bakau at tropic Bungalow [UTM 28PCK1790], swept in meadow rich in flowers, at the beach, leg. Cederholm, Daniellson, Hammarstedt, Hedqvist, Samuelsson, coll. MZLU; 1♀, 16.x.1999, Kiang West National Park, headquarter, leg. W. Schacht, coll. ZSMC; IVORY COAST: 1♀, 9.xi.1983, Badenous Mbingué [9.50°N 5.50°W], leg. R. Summkeller, coll. ZFMK; KENYA: 1♂, 27.iv.2008, Nguni, n of Ngomeni, hand net, leg. M. Snížek, coll. PMME; 2♂♂, 29.iv.1995, Tsavo East, leg. R. Copeland, coll. NMKE; 1♂, 10. vi.1998, Tsavo East National Park, near Athi River [2°37'S 38°22'E], leg. R. Copeland, coll. NMKE; 1♂, 22.v.2006, Coast Province, Tsavo East National Park, near Galana River [UTM UTM 37 m 503352 9665277], 246 m, hand net, leg. P. Cerretti, D. Avesani, G. Carpaneto, G. Nardi, coll. PMME; 1♀, 26.-29.vi.1999, Eastern Province, at Athi river [2°38.51'S 38°21.98'E], Malaise trap, leg. R. Copeland, coll. IITA; 1♂, 17.-31.viii.2005, Nyanza Province, Ungoye, ICIPE Field Station [0.61325°S 34.08908°E], 1127 m, leg. R. Copeland, coll. NMKE; 1♂, 26.vi.-10.vii.2007, Rift Valley Province, Sumburu Nature Reserve, near Ewaso Ng'iro River [0.56797°N 37.53563°E], 874 m, Malaise trap, riverine forest next to headquarter, leg. R. Copeland, coll. NMKE; 1♂, 12.-26.vi.2006, ditto; 1♂, 10.iv.1998, Samburu District, Samburu Serena Lodge, leg. R. Copeland, coll. NMKE; LESOTHO: 1♂, 1.xi.1949, Mamathes [-29.136617 27.845796], leg. C. Jacot-Guillarmod, coll. AMGS; MADAGASCAR: 1♀, 8.xi.2003, Anteninde, Sakahara [22°53'57"S 44°28'12"E], 395 m, leg. A. Ssymank, coll. PASS; 1♂, v.1937, Bekily, leg. A. Seyrig, coll. MNHN; 1♂, iv.1937, ditto; 1♂, v.1937, ditto; 1♂ 1♀, iv.1942, Bekily, det. as *P. madagascariensis* by Camras 1960, leg. A. Seyrig, coll. MRAC; 2♂♂, 9. iv.1994, Berenty reserve 80 km w of Port-Dauphin [25°00'S 46°18'E], leg. M. Wasbauer, coll. UCDC, PMHA; 1♀, 6.xi.2003, Ihasofotsy-Flussufer, ca 10 km wsw Ihosy [22°25'16"S 46°00'14"E], 1000 m, leg. A. Ssymank, coll. PASS; 1♂, 19.iii.1994, Isalo, Analalava, leg. A. Pauly, coll. MRAC; 1♀, 25.ii.-3.iii.1968, Majun-



- ga s. l., det. as *P. madagascariensis* by Camras 2000, leg. K. M. G. & P. D., coll. NHML [NHMUK010922098]; 1♂, i.1992, Morarano-Chrome [17°45'S 47°59'E], leg. A. Pauly, coll. MRAC; 1♂, no date, Sambirano, leg. [?], coll. ZMHB; 1♀, no date, Tananarivo, det. as *P. madagascariensis* by Camras 1960, [collector unknown], coll. MRAC; 1♀ 1 specimen, i.1952, Tzimbazaza-Tananarive, det. as *P. madagascariensis* by Camras 1960, leg. R. Benoist, coll. MRAC; 1♀, 28.vii.–vi.viii.2001, Diego-Suarez (Antsiranana), Sakalava Beach, malaise across sandy trail in dwarf littoral forest [12°15'46"S 49°23'51"E], 10 m, leg. R. Harin'Hala, coll. CAS; 1♂, 4.i.2007, Mahayanga Province, 20 km nw Borinziny [15°27.07'S 47°36.85'E], 37 m, hand netted in tropical dry forest on white sand, leg. M. E. Irwin, F. D. Parker, R. Harin'Hala, coll. CAS; 1♀, 1.xi.1993, Tamatave (Toamasina), Analmalotran Tamatave, leg. C. F. Kassebeer, coll. PCFK; 1♀, 12.xii.1991, Tuléar (Toliara), Ampanihy, leg. A. Pauly, coll. MRAC; 1♀, 6.–16.i.2003, Tuléar (Toliara), Andoha National Park, Parcel II, Tsimela, malaise trap in transitional forest, 175 m [24°56.21'S 46°37.60'E], leg. M. E. Irwin, F. D. Parker, R. Harin'Hala, coll. CAS; 1♂, 12.iv.1968, Tuléar (Toliara), Bevilany, 300 m, det. as *P. madagascariensis* by Camras 2000, leg. K. M. G. & P. D., coll. NHML [NHMUK010922097]; 1♀, 8.–18.vi.2002, Tuléar (Toliara), Beza Mahafaly Reserve, malaise in dry deciduous gallery forest, 165 m [23°41.19'S 44°35.46'E], leg. R. Harin'Hala, M. E. Irwin, coll. CAS; MALI: 1♀, 20.viii.1991, 10 km s Mopti, leg. M. Schwarz, coll. PMHA; 1♂, 20.viii.1991, 10 km s Mopti, sweep netting, leg. M. Schwarz, coll. PMHA; 1♂, 31.vii.1991, 40 km sw Segou, sweep netting, leg. M. Schwarz, coll. PMHA; MOZAMBIQUE: 2♂♂, 12.–20.xii.2003, Manica Province, 45 km nw Chimoio, leg. J. Halada, coll. CULSP; NAMIBIA: 1♀, 28.i.1993, 100 km sw Rundu, leg. M. Schwarz, coll. PMHA; 2♀♀, 16.i.1993, 125 km sw Rundu, leg. M. Schwarz, coll. PMHA; 2♀♀, 16.i.1993, ditto; 2♂♂, 4.ii.1993, 15 km e Swakopmund, sweep netting, leg. M. Schwarz, coll. PMHA; 2♂♂, 29.iii.2000, 18 km se Stampriet C15 to Gochas [24.28°S 18.30°E], visiting pink flowers of *Galenia*, leg. F. W. Gees, S. K. Gees, coll. AMGS; 2♂♂, 4.ii.1990, 30 km e Windhoek, sweep netting, leg. M. Schwarz, coll. PMHA; 1♂, 12.iii.2014, 35 km w Gobabis [22°23'S 18°39'E], 1480 m, leg. J. Halada, coll. CULSP; 1♂, 16.ii.1990, 40 km w Witvlei, leg. M. Schwarz, coll. PMHA; 1♂, 16.ii.1990, 40 km w Witvlei, sweep netting, leg. M. Schwarz, coll. PMHA; 1♂, 11.iii.–9.iv.1985, 6 km n Arandis, Damaraland [22°22'S 14°59'E], leg. J. Irish, H. Rust, coll. SMWN; 1♀, 21.i.1993, 60 km E Rundu, leg. M. Schwarz, coll. PMHA; 1♂, 13.ii.1990, 73 km s Mariental, sweep netting, leg. M. Schwarz, coll. PMHA; 3♀♀, 25.ix.1997, e Oranjemund 28 km from checkpoint to Sendelingsdrif [29.26°S 16.42°E], on yellow flowers of *Deverradenudata* (Viv.) Pfisterer & Podl., leg. F. W. Gees, S. K. Gees, coll. AMGS; 2♂♂, 20.xii.1995, Etosha National Park, 50 km ne Okaukuejo, "Salvado" [18.9°S 16.5°E], leg. C. Schmid-Egger, coll. PMHA; 1♀, 16.–19.i.2007, Gobabeb, Kuiseb-Tal, at light, leg. Mey, Ebert, coll. ZMHB; 1♀, 11.ii.1993, Okahandja, leg. M. Schwarz, coll. PMHA; 1♀, 7.iii.1999, Karas Mountains, 6 km s on 201 from 26 [27.09°S 19.01°E], on yellow flowers of *Vahlia capensis* (L. f.) Thunb., leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 25.iv.1972, Karasburg, Warmbad, SE 2818 Ba, [collector unknown], coll. SMWN; 1♂, 17.–19.v.1978, Khowarib, R., SE 1914 Ac, Kackoland, leg. S. Louw, M.-L. Penrith, coll. SMWN; 1♂, 12.–14.iv.1974, Mukorob 14, Namaland, SE 2918 Ac, [collector unknown], coll. SMWN; 1♂, 15.iii.1997, near Aus on road to Helmeringhausen [26.37°S 19.20°E], visiting white flowers of *Psilocaulon göareosum* (Berger) Dinter & Schwantes, leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 10.–13.ii.1972, Otjikoko-Sud 61, Omaruru, SE 2116 Ad, [collector unknown], coll. SMWN; 1♂, 4.–5.iii.1972, Plateau 38, Luderitz, SE 2616 Cb, [collector unknown], coll. SMWN; 1♂, 27.iv.1972, Rotegab 95, Keetmanshoop, SE 2718 Ad, [collector unknown], coll. SMWN; 1♀, 11.iv.1998, Swakop River bed on road to Goanikontes [22.41°S 14.35°E], on white flowers of *Psilocaulon salicornioides* (Pax) Schwantes, leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 11.iv.1998, Swakop River bed on road to Goanikontes [22.41°S 14.35°E], visiting deep pink flowers of *Gelenia papulosa* (Eckl. & Zeyh.) Sond., leg. F. W. Gees, S. K. Gees, coll. AMGS; 2♂♂, 11.iv.1998, Swakop River bed on road to Goanikontes [22.41°S 14.35°E], visiting white flowers of *Psilocaulon salicornioides* (Pax) Schwantes, leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 11.iv.1998, Swakop River bed on road to Goanikontes [22.41°S 14.35°E], visiting yellow flowers of *Zygophyllum simplex*, leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♀, 16.iii.1999, Swakopmund, Swakop River at bridge [22.42°S 14°32'E], on white flowers of *Zygophyllum stapffii* Schinz, leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 13.iv.2002, Walfisbay, Swakopmund via Dune 7 [22.55°S 14.36°E], leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♀, 20.–23.xii.1974, Windhoek, Wasservallei [22°55'S 16°22'E], [collector unknown], coll. SMWN; 1♀, 6.–8.ii.2001, Gobabis District, Somerkoms 521 [22°01'59"S 19°57'22"E], leg. A. H. Kirk-Spriggs, coll. SMWN; 1♀, 20.iii.2014, Harda Province, 15 km s Rehobot [23°28'S 17°07'E], 1400 m, leg. J. Halada, coll. CULSP; 2♂♂, 16.ii.1990, Omaheke Region, Gobabis, 40 km w Witvlei, leg. M. Schwarz, coll. PMHA; 1♀, 25.–27.iii.2003, Rundu District, Mile 46 [18°18'39"S 19°15'29"E], leg. A. H. Kirk-Spriggs, coll. SMWN; SENEGAL: 1♂, 27.vi.2004, 60 km s Velingara, sweep netting, leg. M. Halada, coll. CULSP; SOUTH AFRICA: 1♂ 2♀♀, 8.–12.ii.1982, Sandveld Nature Reserve, Hoopstad, SE 2725 Da, leg. Entomology Department, coll. BMSA; 1♂, xii.1956, [?] "Snoot Rivien", leg. Martin, coll. AMGS; 1♂, 3.–8.x.1989, Cape Province, 15 km n of

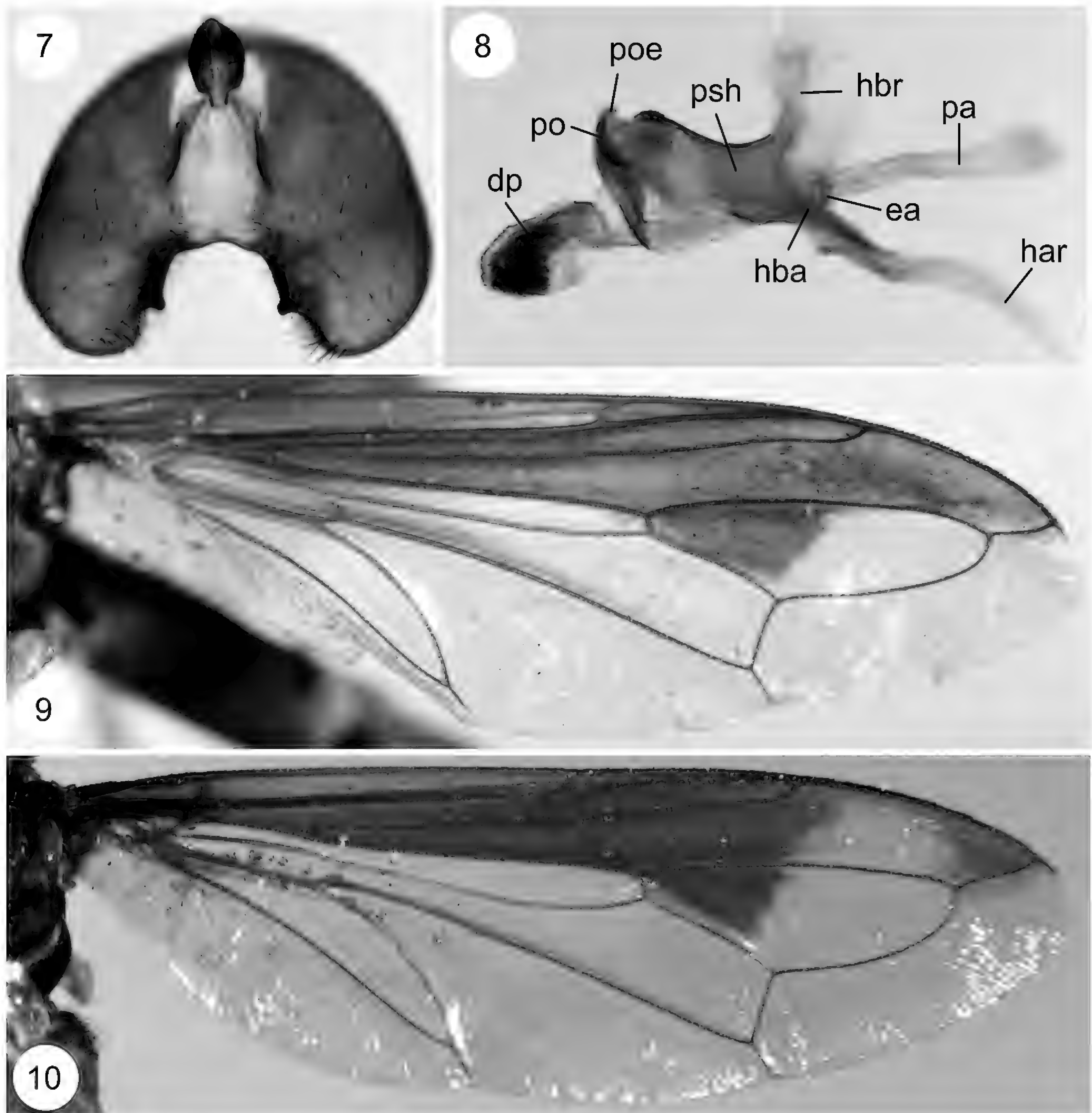


Nieuwoudtville on road to Loeriesfontein, leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♀, 4.i.2010, Cape Province, 25 km n Jansenville [32°49'S 24°44'E], 600 m, leg. J. Halada, coll. CULSP; 1♀, xii.1922, Cape Province, Aliwal North, det. as *P. brevistylatus* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922102]; 1♀, 3.xii.1986, Cape Province, Bloutoring [33°28'40"S 20°19'15"E], leg. F. W. Gess, coll. AMGS; 1♀, 24.xii.1960, Cape Province, Grahamstown, leg. E. McC Callan, coll. AMGS; 1♀, 27.xi.1981, Cape Province, Grahamstown, [?] "Olakwater", leg. F. W. Gess, coll. AMGS; 1♀, 13.i.1986, Cape Province, Grahamstown, Clifton, leg. R. W. Gees, coll. AMGS; 1♀, 12.–30.i.1970, Cape Province, Grahamstown, Hilton [-33.310629 26.525595], Malaise trap, leg. F. W. Gess, coll. AMGS; 1♂, 3.iii.1978, Cape Province, Grahamstown, Hilton [-33.310629 26.525595], on flowers of *Melolobium candidans* in sandpit, leg. F. W. Gess, coll. AMGS; 1♂, 3.iii.1978, Cape Province, Grahamstown, Hilton [-33.310629 26.525595], leg. S. K. Gess, coll. AMGS; 1♂, 2.xii.1989, Cape Province, Grahamstown, Hilton [-33.310629 26.525595], leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♀, 22.x.1981, Cape Province, Grahamstown, Lynton, leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 12.ii.1967, Cape Province, Grahamstown, Strowahn, leg. C. Jacot-Guillarmod, coll. AMGS; 1♂, 19.–24.iii.191[?], Cape Province, Grahamstown, Table Farm, leg. F. W. Gess, coll. AMGS; 1♂ 1♀, 2.–13.iii.2008, Cape Province, Grahamstown, Three Chimneys Farm [33°18.542'S 26°29.846'E], leg. A. H. Kirk-Spriggs, coll. AMGS; 1♂, 11.x.1994, Cape Province, Hamaqual and Kamieskroon / Sors Sors, leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 17.–21. & 24.ix.1995, Cape Province, Richtersveld National Park, Koeroegabvlakte [28.11°S 17.03°E], visiting deep pink flowers of *Hermbsstaetia glauca* (Wendl.) Reichb. ex Steud., leg. F. W. Gess, S. K. Gees, R. W. Gess, coll. AMGS; 1♂, 15.ix.1996, Cape Province, Richtersveld, Pachtviel [28.33°S 16.34°E], leg. F. W. Gess, S. K. Gess, R. W. Gess, coll. AMGS; 1♂, 16.xi.1994, Cape Province, Tierberg [33.10°S 22.16°E], visiting cream flowers of *Asclepias buchenaviana* Schinz, leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 26.xi.–5.xii.1987, Cape Province, Tierberg, research station [33°7'42"S 22°16'24"E], leg. F. W. Gess, S. K. Gess, R. W. Gess, coll. AMGS; 1♀, 26.xi.–25.xii.1987, Cape Province, Tierberg, study site [33°10'S 22°16'24"E], on flowers of *Asclepias buchenaviana* Schinz, leg. F. W. Gess, S. K. Gess, R. W. Gess, coll. AMGS; 6♂♂, 26.xi.–5.xii.1987, Cape Province, Tierberg, study site [33°10'S 22°16'24"E], visiting flowers of *Asclepias buchenaviana* Schinz, leg. F. W. Gess, S. K. Gess, R. W. Gess, coll. AMGS; 1♀, 1.-9-xii.1988, Cape Province, Vanwyksfontein, 8 km w of Norvalspont, leg. R. W. Gees, coll. AMGS; 1♀, 12.i.2004, Eastern Cape Province, Grahamstown, [33°16'00"S 26°28'60"E], 629 m, leg. C. Hepburn, coll. AMGS; 1♂, 10.x.1992, Eastern

Cape Province, Grahamstown, Hoowisonspoort, 3326 BC, leg. T. Doubel, coll. AMGS; 1♂, 28.ii.2004, Eastern Cape Province, Thomas Baines Nature Reserve [33°23'02'S 26°29'01"E], leg. C. C. Robertson, coll. AMGS; 1♀, no date, Eastern Cape Province, Willowmore, leg. Brauns, coll. PJHS; 1♂, xii.1907, Eastern Cape Province, Willowmore, det. as *P. interrupta*, leg. H. Brauns, coll. MRAC; 1♀, no date, Eastern Cape Province, Willowmore, det. as *P. interrupta*, leg. H. Brauns, coll. MRAC; 1♂, 25.i.1902, Eastern Cape Province, Willowmore, leg. Brauns, coll. PJHS; 1♀, 25.–29.x.2010, Free State Province, Brandfort, Florisbad Res. Stat. [28°46.039'S 26°04.234'E], leg. A. H. Kirk-Spriggs, coll. BMSA; 2♀♀, 8.–12.ii.1982, Free State Province, Hoopstad, Sandfeld Nature Reserve, SE 2725 Da, leg. Entomology Department, coll. BMSA; 1♀, 13.xii.1995, Mpumalanga Province, Blyderevierspoort NP [24°39'S 30°50'E], leg. F. Koch, coll. ZMHB; 1♂, 1.x.1997, Northern Cape, 60 km e Springbok [29.28°S 18.26°E], visiting cream flowers of *Asclepias buchenaviana* Schinz, leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 10.x.2000, Northern Cape, Pachtvlei, e Alexander Bay [28.33°S 16°34'E], visiting yellow flowers of *Lebeckia*, leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 20.xi.1999, Western Cape Province, 7 km n of Avontuur [33°40'S 23°09'E], sweep netting, leg. M. Hauser, coll. PMHA; 1♀, 11.iv.2006, Western Cape Province, Stellenbosch [33°55'S 18°51'E], leg. E. Mostert, coll. AMGS; SUDAN: 1♂, 14.vi.1996, Blue Nile, Wad Medani, leg. G. G. M. Schulten, coll. RMNH; 1♂, 1935, Sangha près Bandiagara, leg. M. Griaule, coll. MNHN; TANZANIA: 1♀, 16.i.2007, Pwani Province, 15 km e Utete [08°03'S 38°53'E], 75 m, leg. J. Halada, coll. CULSP; TOGO: 2♀♀, 7.iv.2008, Mono riverside s Ahassomé [7°11'14"N 01°28'52"E], 90 m, leg. A. Ssymank, coll. PASS; ZAMBIA: 1♀, 27.vii.–13.viii.1910, Upper Luangwa River, des. as syntype of *P. decisa*, leg. S. A. Neave, coll. NHML [NHMUK010922107]; 5♂♂, 20.v.–29.vii.1988, Zambezi Valley [16°18'S 30°16'E], leg. J. Weyrich, coll. ZFMK; ZIMBABWE: 1♂ 4♀♀, 18.–19.xii.2011, 60 km nnw Bulawayo [19°41'S 28°21'E], 1200 m, leg. J. Halada, coll. CULSP; 1♀, 14.xii.1919, Bulawayo, des. as syntype of *P. decisa*, [collector unknown], coll. NHML [NHMUK010922108]; UNKNOWN LOCATION: 1♀, 24.i.1928, "Rersolution", leg. A. Walton, coll. AMGS; 1♀, 1893, "Shitlesia", leg., coll. AMGS; 1♂, no date, "T287", [collector unknown], coll. ZFMK; 1♂, no date, "T426", [collector unknown], coll. ZFMK.

Stuke (2015b) concluded that *P. antiqua* is an outstandingly variable species and as a result several new synonyms were recognised in the Palaearctic Region. While reviewing the large amount of material available it became evident that most of the commonly occurring Afrotropical *Physocephala* specimens also belong to the *antiqua* species-group. It cannot be excluded that factors





**Figs 7–10.** *Physocephala antiqua* (Wiedemann, 1830). 7. Epandrium, dorsal view (♂, Namaqualand and Kamieskroon); 8. Hypandrium and phallus, lateral view (♂, Namaqualand and Kamieskroon); 9. Wing, darker form, ventral view (♀, Clifton, Grahamstown); 10. Wing, paler form, ventral view (♀, Badenou s Mbingué). dp = distiphallus; ea = ejaculatory apodeme; har = hypandrial arms; hba = hypandrial bars; hbr = hypandrial bridge; pa = phallapodeme; po = postgonite; poe = postgonite evagination; psh = phallus sheath.

such as DNA-sequencing, newly discovered morphological characters or the host ranges of larvae may eventually necessitate the splitting of *P. antiqua* as defined herewith but at the present time the consistent separation of distinct species within this highly variable taxon is not possible using the morphological characters which are

currently available, or which have been used in the past. We could not find any consistent differences in the male postabdomen or female theca within the various morphs, for example, and the Afrotropical material is highly variable in respect of characters such as wing pattern and microtrichiation, size and shape of the vertex, dusting



and setulae on the pleura, body size, and colouration of the legs, abdomen and thorax. Dark-winged specimens with the basal cell almost completely covered with microtrichia (although never completely covered!) appear remarkably distinct, but we also found intermediates. Such specimens could potentially be incorrectly assigned to the newly described *P. guillarmodi* (see below) although the dark brown subcosta of *P. antiqua* (light orange-brown or yellow in *P. guillarmodi*) and the more or less black scutellum (orange in *P. guillarmodi*) are good characters for separating these two species. *Physocephala antiqua* specimens with a shortened radial-medial crossvein appear very similar to species of the *microvena* species-group, but always lack a distinct shining indentation at the hind margin of the eye and have a different male postabdomen. Specimens in which the pleural dusting stripe is indistinct, such as in old specimens or specimens which have been wetted, could very easily be misidentified as belonging to the *vittata* species-group.

*Physocephala maculipes* has previously been described as a very variable species (Camras 2001). We cannot find any differences to distinguish Afrotropical specimens previously reported as *P. maculipes*, nor the examined holotype, from Palearctic specimens which have been identified as *P. antiqua*. Therefore, *Physocephala* [*Conops*] *maculipes* Bigot, 1887 is herewith placed as a junior synonym of *Physocephala* [*Conops*] *antiqua*

Wiedemann, 1830 (**syn. nov.**). Consequently, all previous synonyms of *P. maculipes* are also now placed as synonyms of *P. antiqua* (see Stuke 2017a).

*Physocephala madagascariensis* Kröber, 1915 is the only species of the genus reported from Madagascar to date. This is also described as being a very variable species (Camras 1962a) and in our view cannot be distinguished from *P. antiqua*, and therefore it is also herewith placed as a junior synonym to *Physocephala* [*Conops*] *antiqua* Wiedemann, 1830 (**syn. nov.**). This is the only species known from Madagascar, so there should be no doubt concerning the identification of specimens.

Kröber (1939) had previously assumed that his *P. minutissima* was no more than a small, dark morph of *P. interrupta* Bezzi, 1901 (= *P. antiqua*). We examined the male holotype, hitherto the only known specimen of this species, which is in very bad condition with both wings and abdomen lost. We also have specimens of small and dark Afrotropical *P. antiqua* which fit completely with the original description of *P. minutissima*, as well as with the remaining parts of the holotype. *Physocephala minutissima* Kröber, 1933 is therefore also herewith placed as a junior synonym to *Physocephala* [*Conops*] *antiqua* Wiedemann, 1830 (**syn. nov.**).

*Physocephala gracilia* Kröber, 1915 has so far only been known from two syntype specimens. Camras (2001) considered that *P. gracilia* might be synonym of *P. mac-*



Fig. 11. Habitus of *Physocephala brevipennis* Camras, 1962 (holotype).



*ulipes* Bigot, 1887 (= *P. antiqua*) and in fact almost all the characters given both in the original description and in the additional information provided by Camras (2001) fall within the variability of *P. antiqua*. We also have other specimens to hand which fit completely with the original description. The only anomalous characters in the original description are the short proboscis, completely black claws and shining tergites 1–3, which have not been found to date in material of *P. antiqua*. These characters were not mentioned in the key of Kröber (1915), however, nor in the subsequent comments of Camras (2001), and are not evident in any the material which we have to hand. One syntype is probably destroyed (Stuke 2017a) whilst the second is held at the Museo Civico di Storia Naturale “Giacomo Doria” but was not available for examination. In the absence of better information we therefore believe the best current solution for this cryptic taxon is to place *Physocephala gracilia* Kröber, 1915 as a junior synonym of *Physocephala* [*Conops*] *antiqua* Wiedemann, 1830 (**syn. nov.**).

***P. brevipennis* Camras, 1962**

(Fig. 11)

*Physocephala brevipennis* Camras, 1962

**Primary type material examined.** ♂ holotype of *Physocephala brevipennis* Camras, 1962: (1) “Ngutu, / Zululand / III-21-1951 / A. L. Capener”; (2) “*Physocephala brevipennis* / Camras”; (3) “Holotype ♂ / *Physocephala brevipennis* / Camras”; (4) “FMNHINS / 3130492 / Field Museum / pinned”; coll. FMNH.

The first impression when looking at this strange specimen is that it is perhaps an aberrant example of *Physocephala antiqua* with exceedingly shortened wings. Until

further material becomes available, however, we have retained this taxon.

***P. claripennis* Becker, 1923**

(Fig. 12)

*Physocephala claripennis* Becker 1923

**Primary type material examined.** ♂ holotype of *Physocephala claripennis* Becker, 1923: (1) “El Obeid / 13.–14. III”; (2) “Aegypt. Sudan / Ebner, 1914”; (3) “*Ph. claripennis* [sic] / Beck. / det. Becker”; (4) “Holotype / *Physocephala claripennis* / Becker / det. Camras, 2000”; (5) “J. Skevington / Specimen # / 45425”; coll. NMW.

This may only be an extremely pale specimen of *P. antiqua* with completely hyaline wings, but until further material becomes available we have retained this taxon.

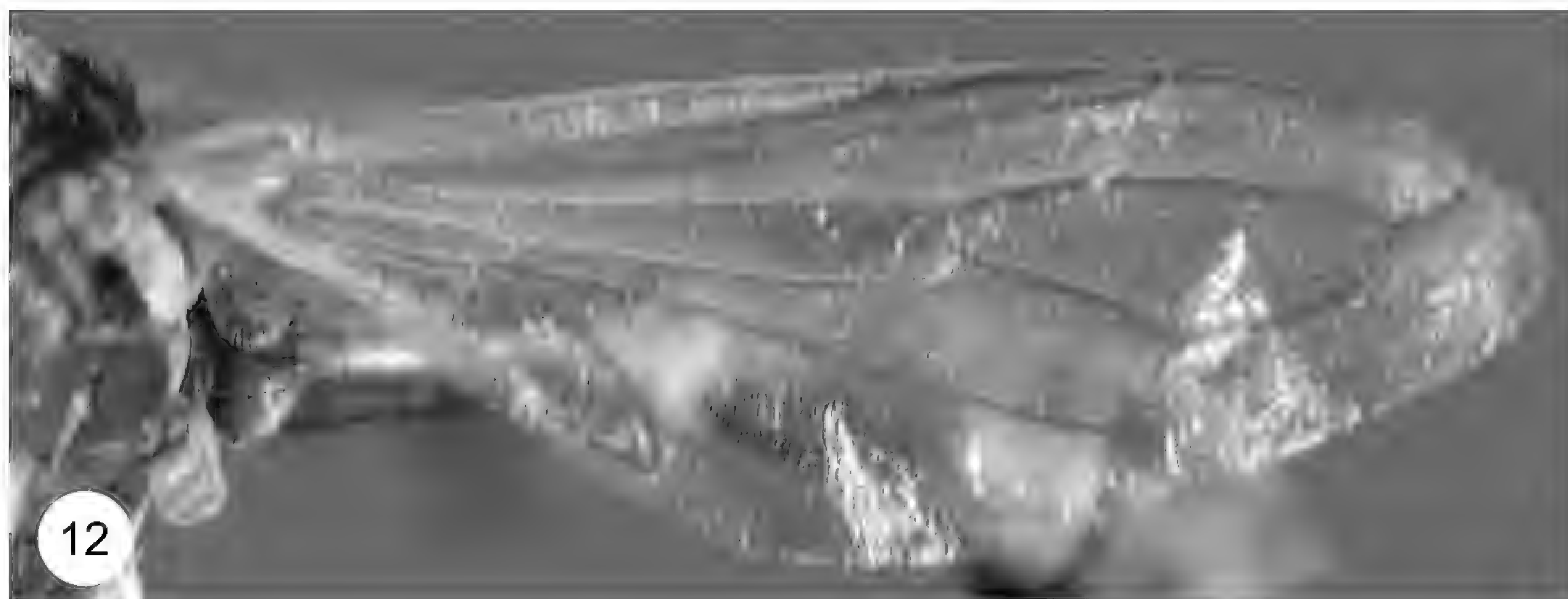
***P. guillarmodi* spec. nov.**

(Figs 13–24)

urn:lsid:zoobank.org:act:8F911A66-CF42-4A60-837F-708FA78B1E9C

**Holotype** ♀. (1) “Mamathes / Basutoland / 28-XII-1959 / C. Jacot / Guillarmod”; (2) “? *Physocephala brevistylata* / Kröber ♀”; (3) Holotypus / *Physocephala guillarmodi* / spec. nov. ♀ / 2018”. Holotype is deposited in AMGS. The specimen is pinned and in perfect condition.

**Paratypes.** BURUNDI: 1♀, 18.xi.1949, Bururi Province, Bururi, 1950 m, Orée dela forêt, leg. F. François, coll. ISNB; LESOTHO: 1♂, 26.xii.1946, Bokong, leg. A. Jacot Guillarmod, coll. AMGS; 1♀, 28.xii.1947, Leribe, Hensley's Dam, leg. A. Jacot-Guillarmod, coll. AMGS; 1♀, 16.xii.1950, Mamathes, leg. C. Jacot-Guillarmod, coll. AMGS; 1♂, 28.xii.1959, ditto; SOUTH AFRICA: 1♂, 3.–7.x.1988, Cape Province, Clanwilliam



**Fig. 12.** Wing of *Physocephala claripennis* Becker, 1923 (holotype).

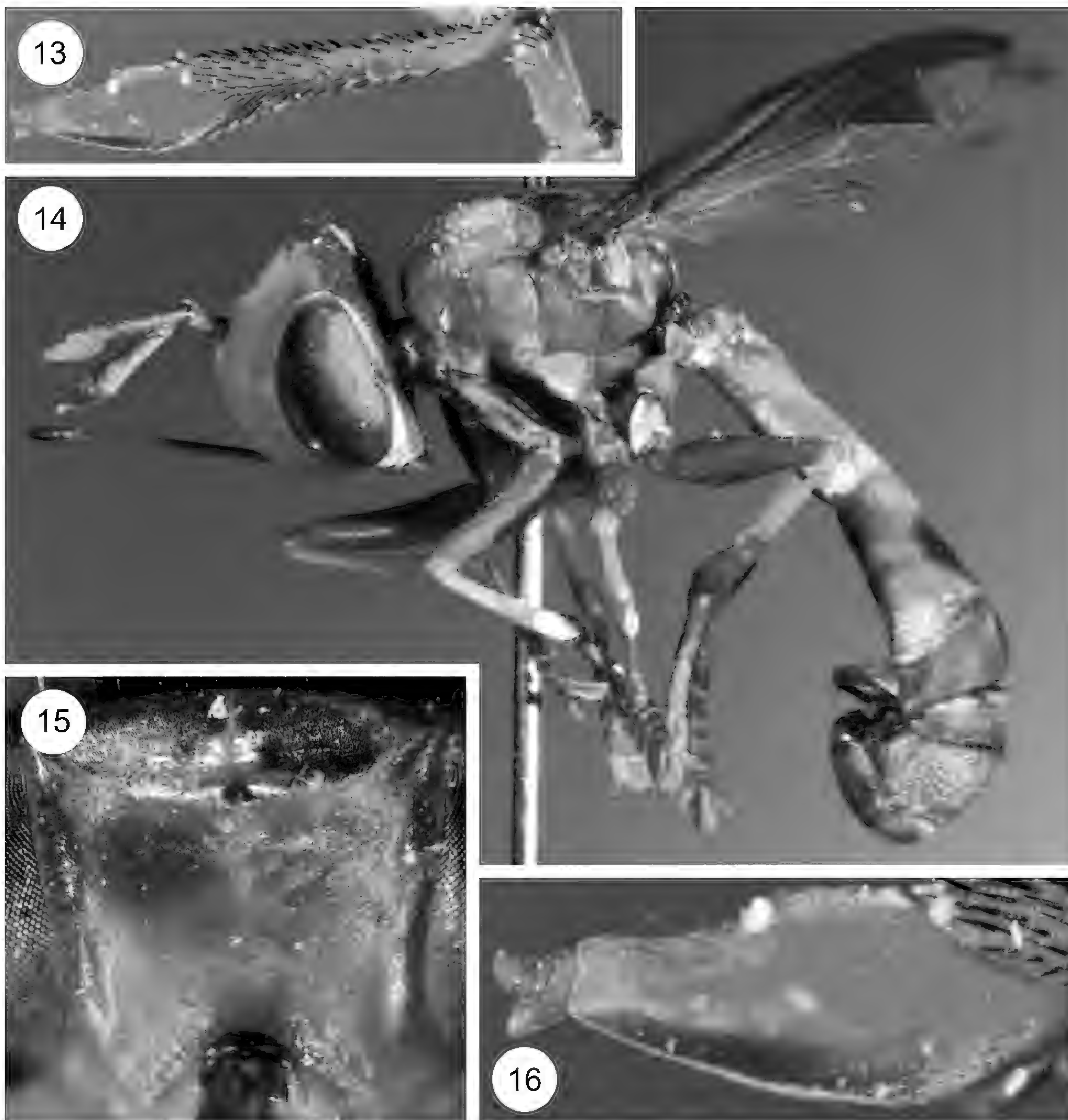


Dam [32°11'30"S 18°53'42"E], on flowers of *Aspalathus desertorum* Bol., leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂, 5.xii.1980, Cape Province, Grahamstown, Hilton, *Senecio*, leg. D. W. Gees, coll. AMGS; 1♀, 8.–13.x.1987, Cape Province, Klein Alexandershoek, Clanwilliam District [32°20'20"S 18°46'E], leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♂ 1♀, 28.ix.1985, ditto; 1♂, 4.–8.x.1994, Cape Province, Koornplanskloof 10 km s Citrusdaal [32°40'S 19°01'E], 200–270 m, leg. R. Danielsson, coll. MZLU.

#### Description of holotype (female)

Length 9.6 mm; Wing-length 7.6 mm; Head-height 2.9 mm.

**Head.** Antenna orange-brown (Fig. 13). Arista very short stylus-like, with 2 aristomeres situated at tip of first flagellomere (Fig. 16). Both aristomeres minute, length of apical aristomere shorter than height. Scape about twice as long as maximum width, apically and laterally with black setae. Pedicel about five times longer than maximum width, covered with black setae. Pedicel lack-



**Figs 13–16.** *Physocephala guillarmodi* spec. nov. (holotype). **13.** Antenna, lateral view; **14.** Habitus, lateral view; **15.** Frons, dorsal view; **16.** Arista, lateral view



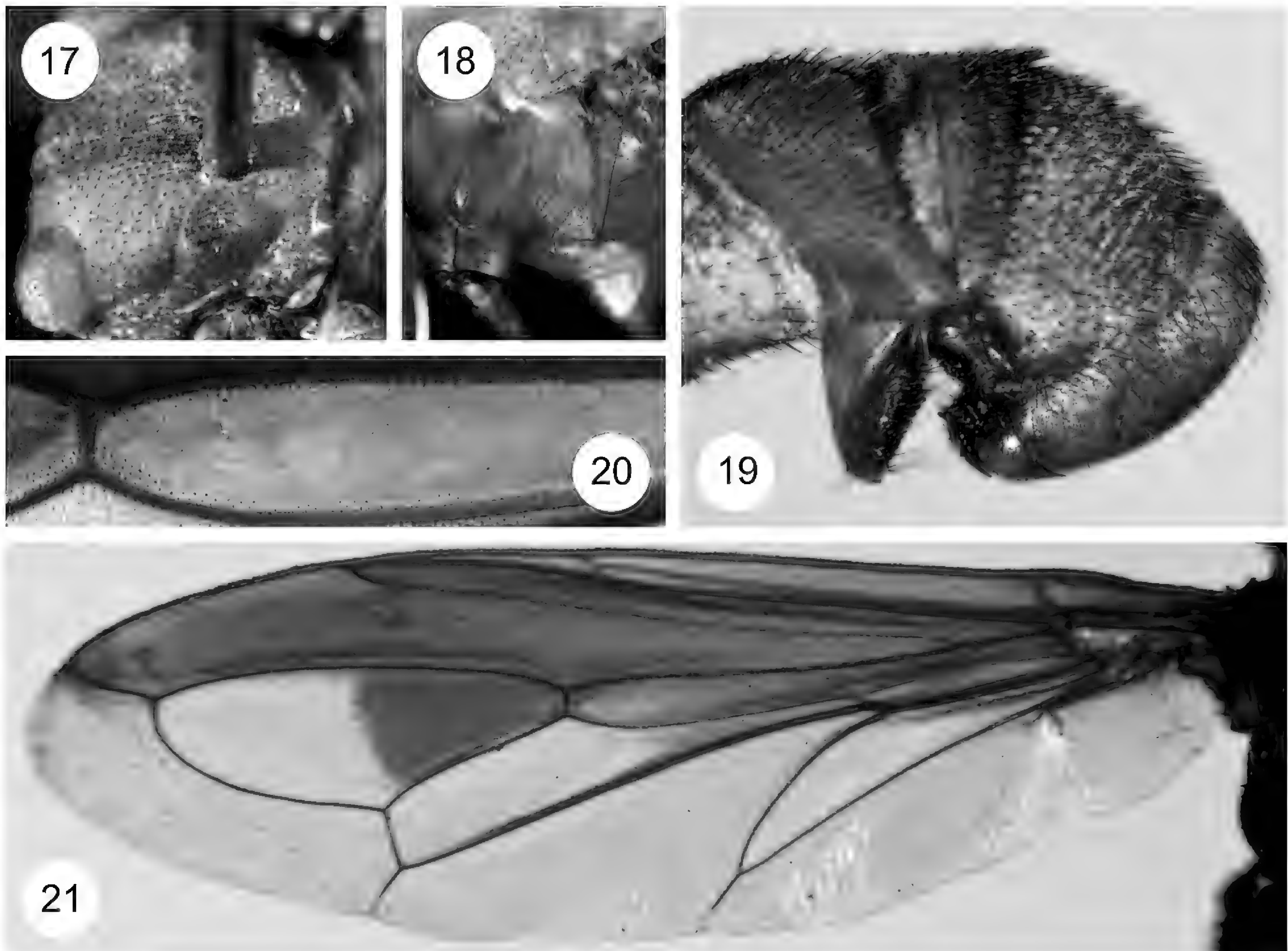
ing any ridge at base, and expanded towards apex. First flagellomere long and conical, about two times as long as high, pointed, and ventrally with an indistinct membranous area. Lunule between base of antennae and ptilinal suture distinctly developed, shorter than width of scape. Eyes brown, lacking ommatrichia, facets all of about the same size. Posterior margin of eye lacking any shining indentation. Gena height / eye height (measurements taken from head in lateral view) = 0.3. No ocellar tubercle, no ocelli and no ocellar triangle evident. Frons (Fig. 15) yellow, somewhat broader than long, concave, slightly projecting above eyes posteriorly and lacking any setulae. Anterior margin of frons concave. No frontofacial spot. Frons with indistinct dusting all over, subshining laterally. Vertex as broad as frons, separated from latter by a more or less distinct ridge. Vertex shining, and in posterior half covered with black setulae. Vertex apically with an indistinct depression. Ridge of vertex lacking longitudinal grooves. Face yellow, with brown facial keel. Face lacks dusting except for some very narrow silver dusting along eye margin. Gena yellow, lacking setae. Distinct facial grooves reaching mouth edge. Distinct facial carina reaching from base of antennae to a distinctly broadened and outstanding frontoclypeal tubercle. Ptilinal suture extending well beneath antennal bases on either side. Oral cavity tapers dorsally. Postcranium not obviously invaginated, yellow to light brown. Whole postcranium lightly dusted, with dusting adjacent to posterior eye margin obviously denser. Occiput and postgena covered with long black setulae. Postgena not widened and not delimited from occiput. Bottom portion of postcranium clearly delimited and less setulose. Proboscis reddish-brown, labellum black. Frontoclypeal membrane long, light orange-brown and barely delimited from orange-brown clypeus. Palps absent. Labium distinctly longer than head-length, distinctly thickened basally, anterior section completely fused and tubular. Labrum not visible in type specimen. Labellum short, completely divided, hardly broader than adjacent haustellum, and covered with very short setulae only.

**Thorax** mainly orange-brown, with mediotergite, katapisternum and meron mainly black. Scutum with large medial black spot and small lateral black spots (Fig. 17). Thorax grey dusted all over. Pleura as in Fig. 18. Distinct dusting stripe on pleura reaching from middle coxa to notopleuron. The dusting stripe depends on the viewing angle and is best seen in dorsal view – care is required as it may be hard to see with the wrong viewing angle (Fig. 18). Anterior half of anepimeron shining to subshining. Presternum distinct, narrow. Basisternum broad, ventrally narrowed to a point, and with scattered setulae. Proepisternum lacks setae or setulae. Notopleuron with a few slightly stronger setae. Postal callus with a few strong short setae flanked laterally by several curved setulae. Katapisternum with 13–15 setae posterodorsally and no setae ventrally. Metakatapisternum lacks

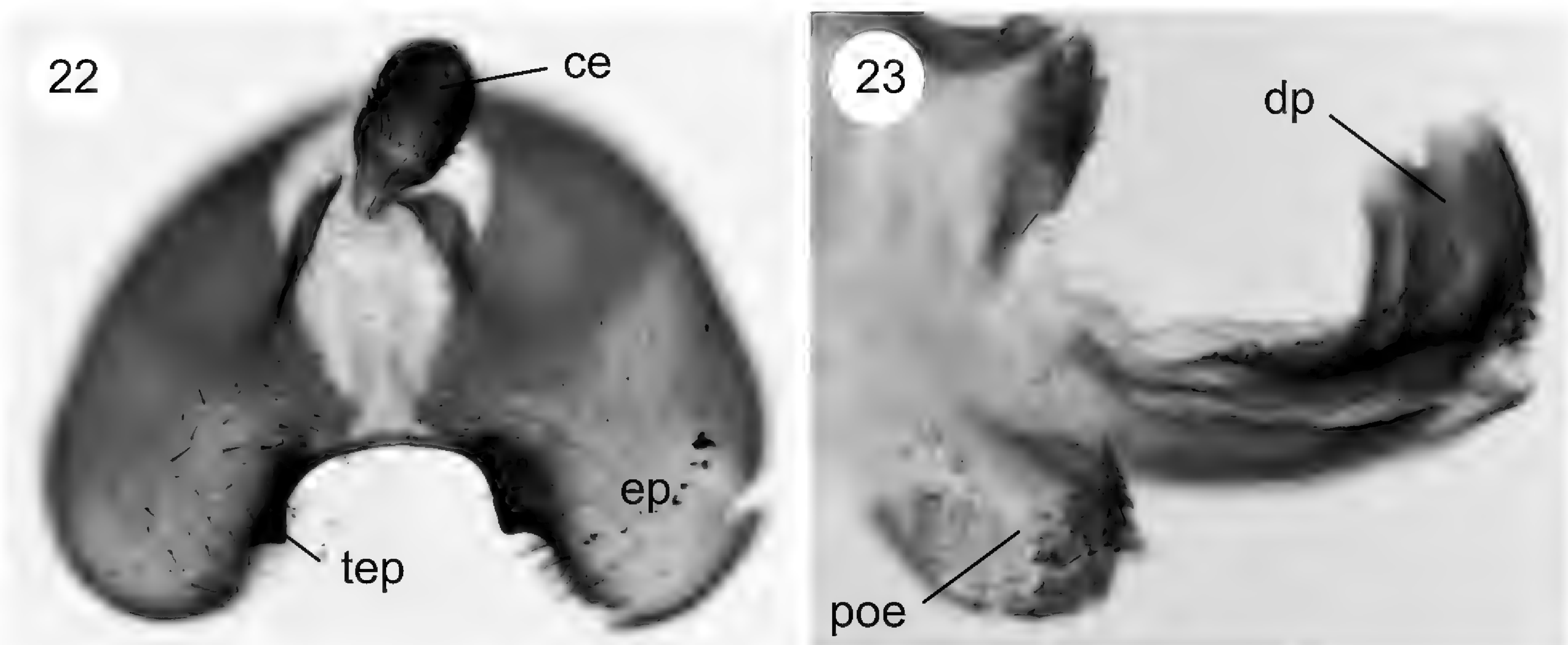
setae. Anepimeron with 8–10 small setulae. Mediotergite convex, with minute and hardly visible black setae. Subscutellum inconspicuous. Scutum covered with scattered small black setulae and with no outstanding setae. Wing as Fig. 21: Fore-margin tinged brown, with brown membrane between subcosta and media M. Cell  $r_{4+5}$  hyaline apically and discal-medial cell dm brown basally. Veins brown, subcosta paler brown than radial veins. Wing mostly covered with microtrichia, but anal lobe partly lacking microtrichia. Radial-medial crossvein rm small but complete (Fig. 20). Basal-medial-cubital crossvein incomplete. Radius  $R_1$  and  $R_{2+3}$  terminate close together in costa, well beyond end of subcosta. Radius  $R_{4+5}$  with shallow, even curve in distal section which is directed towards fore-edge of wing. Cell  $r_{4+5}$  pedunculate, with vein  $R_{4+5}+M_1$  distinctly longer than radial-medial crossvein. Basal cell lacks any thickening. Cubital cell cup elongated, distinctly longer than vein  $A_1+CuA_2$ , and pointed distally (i.e. cubitus  $CuA_2$  and anal vein  $A_1$  meet at an acute angle). Vein  $A_1+CuA_2$  not reaching hind margin of wing. Cubital veins  $CuA_1$  and basal-medial-cubital crossvein distinctly separated. Upper and lower calypters yellowish-white to brown, margin of upper calypter with short white setulae. Alula slightly shorter than broad, lacking setulae on posterior margin. Venae spuriae pronounced in cell  $r_{4+5}$ , cubital cell cup and indistinctly in cubital cell  $cua_1$ . Haltere light yellowish-white with brown base and reddish knob. Knob of haltere with brown setulae. Legs orange with fore coxa mainly black. Legs with inconspicuous silver dusting to shining, hind coxa densely silver-dusted. Posterior surfaces of fore and middle tibiae with obvious silver-dusted fields distally. Legs with short, adpressed black setulae. Base of fore and middle femora lacking denser black setulae. Areas of dense black to brown setulae anteroventrally at tip of fore tibia, and ventrally and posteriorly at tip of hind tibia. Middle femur lacking a distinct row of regularly arranged setulae. Hind femur lacks outstanding setulae. No preapical setae dorsally and no setae ventrally on tibiae. Femora ventrally lacking rows of short black setae. Coxae with several setulae but lacking outstanding setae. Hind femur slightly thickened in basal half. All tibiae thickened in apical half. Each metatarsus with 2 stronger setae ventrally at base. Pulvilli yellowish-white. Claws brown, with narrow black tips. Empodium light brown, about as long as pulvilli.

**Abdomen** orange to dark brown, with diffuse dark markings dorsally on tergites 1–4. Abdomen with short black setulae all over, those on tergite 2 very small. ♀ abdomen completely silver-dusted, although the impression of dusting depends on viewing angle. Denser dusted hind margins of tergites are not obvious. Tergites 1–3 fused but remain distinct from each other. Maximum width of abdomen at segment 4. Length : maximum width of tergite 2 = 2.0; length : maximum width of tergite 3 = 1.9. Tergite 5 and sternite 5 not completely fused laterally.



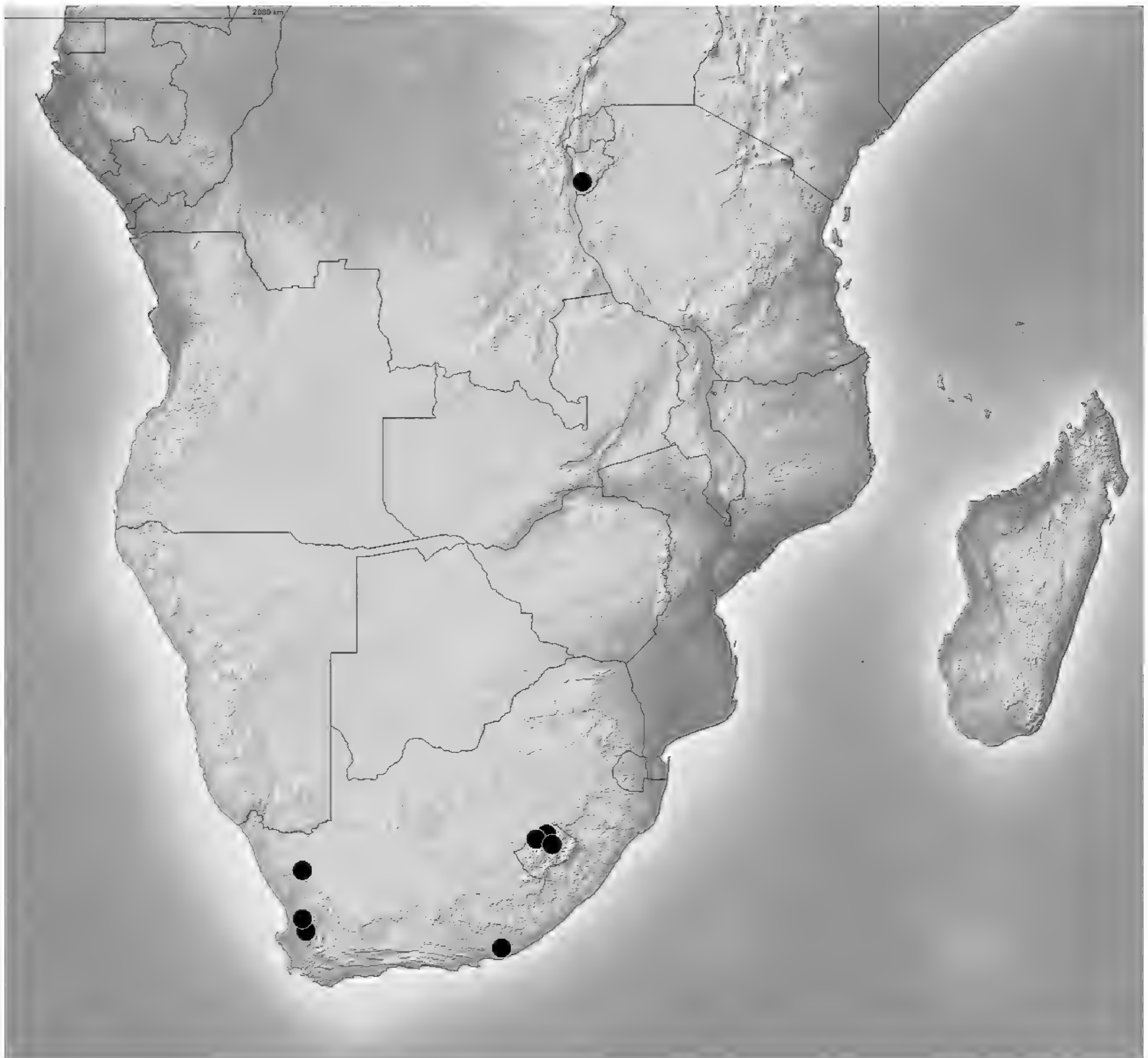


**Figs 17–21.** *Physocephala guillarmodi* spec. nov. (holotype). 17. Scutum, dorsolateral view; 18. Pleura, lateral view; 19. Theca, lateral view; 20. Radial-medial crossvein, dorsal view; 21. Wing, dorsal view.



**Figs 22–23.** Postabdomen *Physocephala guillarmodi* spec. nov. (♂, Hilton, Grahamstown). 22. Epandrium, dorsal view; 23. Postgonite evagination, ventral view. ep = epandrium; dp = distiphallus; poe = postgonite evagination, tep = tooth on posterior margin of epandrium; ce = cercus.





**Fig. 24.** Distribution of *P. guillarmodi* spec. nov.

Shape of theca as shown in Fig. 19. Anterior surface of theca apically with a few long setulae. Posterior surface of theca almost completely covered with close-set long blunt spicules, arranged in about 12 horizontal lines. Tergite 7 bends distinctly ventrally, with an indistinct longitudinal gap, and with a minute protruding tooth at middle of posterior margin.

**Female characters added from one dissected paratype**  
Sternites 1–2 fused. Sternites 3–4 not protruding ventrally, posterior parts of sternites inconspicuous. Tergites 3 and 4 lack evaginations. Sternite 5 anteriorly lacking any elongation. Sternite 6 almost completely covered

with long blunt spicules which are mainly arranged in close-set, broken horizontal lines. Sternite 7 longer than broad, anteriorly pointed, posterior margin with two patches of dense long black setae. Ventral sclerotisation fused with tergite 8 and therefore connecting at sides. Tooth on tergite 8 distinct, its base elongated anteriorly. Sternite 8 bulging posteriorly, covered with strong long black setae and with obvious long setulae on posterior margin. Paired cerci distinct. Sack-like ventral protrusion of vagina with distinct annular sclerotisation. Opposite the annular sclerotisation the ventral protrusion is hardly sclerotised and is covered with short, broad microtrichia giving the ventral protrusion a roughened surface. No ob-



vious sclerotisation at base of either the accessory glands or the spermathecal ducts. Sack-like ventral protrusion of vagina lacks any additional sclerotisation. 2 pairs of spherical spermathecae, the spermathecal ducts fusing shortly after leaving the spermathecae. Spermathecal ducts are sclerotised at the spermathecae, this sclerotised part of the duct being sinuous.

### Description of male

♂ abdomen strongly dusted from posterior half of tergite 3 to tip (in anterior view) and almost shining laterally on tergites 1–3. No obvious dusting at hind margin of tergites. Tergite 1 with obvious black setulae laterally on bulbous lateral projections. Tergite 2 distinctly elongated, about 5 times as long as width at posterior margin. Tergite 2 lacking lateral tufts of setulae. Tergite 3 obviously longer than broad and widened posteriorly, anteriorly about 2.8 times as wide as posteriorly. Sternites 1, 4 and 5 present, sternites 2 and 3 reduced. Tergite 5 and sternite 5 separate. Sternite 4 almost square, minute and not clearly delimited from membrane, with about 4 minute setulae. Sternite 5 apically with small field of thick setae and several long black setulae laterally. Protandrium broader than epandrium and therefore projecting over it. Sternite 8 delimited from protandrium. Line of minute black setulae at border of protandrium and sternite 8. Lateral edges of protandrium fused ventrally by a narrow sclerotised strip, which is not medially broadened. Paired cerci distinct, completely sclerotised and covered with scattered black setulae. Epandrium as shown in Fig. 22, not fused behind cerci but with a slightly sclerotised connection on both sides of the epandrium. Within this connection there is an elongated sclerotisation. Posterior margin of epandrium with small black setulae, and an obvious short black tooth with a broad blackish base. Epandrium distinctly concave laterally. No hypoproct evident and no remains of surstyli recognised. No obvious strong black setae nor long black setulae which would mark the base of a surstylus. Subepandrial plate not sclerotised nor covered with microtrichia, and therefore not distinct. Dorsal hypandrial bridge developed. No hypandrial lobe evident. Hypandrial bars fused distally, hypandrium ending in a hypandrial arm. Hypandrial membrane almost absent, lacking microtrichia. Phallus sheath fused dorsally, lacking any evagination or setulae. Postgonite distinct. Postgonite evagination not sclerotised, and not projecting above distiphallus. Lateral side of postgonite evagination with indistinct microtrichia, the medially directed surface with broad and overlapping microtrichia (Fig. 23). No plate at postgonite evagination. Ring sclerite between phallapodeme and distiphallus indistinct. No epiphallus recognised. Distiphallus shorter than epandrium, entirely covered with microtrichia, some of which are black and arranged in lines. Distiphallus dorsally with large lightly sclerotized plate (Fig. 23) but lacking evaginations. Phallapodeme longer than hypandrium arm. Ejaculatory

apodeme elongated, lacking distinct attachment to sperm sac.

### Variability

Wing length 6.3–7.6 mm. Basal aristomere sometimes black apically. Face, gena, frons and postcranium sometimes more or less black in melanistic specimens. Facial keel sometimes yellow. Extent of black marking on thorax varies somewhat, and scutum sometimes completely orange. Proepisternum may lack setulae. Wing sometimes more extensively brown, with discal-medial cell dm almost completely brown and cubital cell cua1 brown at base. Alula and cubital cell cup may partly lack microtrichia. All coxae sometimes obviously blackish. Hind femur may have an obscure blackish or brown ring.

### Diagnosis

*Physocephala guillarmodi* belongs to the *antiqua* species-group as defined in Key 1. It is easily overlooked amongst the more common and variable *P. antiqua*, but can be differentiated from the latter by the brown basal cell which is completely covered with microtrichia (Fig. 20). With this character *P. guillarmodi* can only be confused within the *antiqua* species-group with dark-winged specimens of *P. antiqua* which may atypically have the basal cell almost (but never completely) covered with microtrichia, or with *P. pusilla*. *Physocephala guillarmodi* can be separated from both of these species by its light yellow to yellowish-brown subosta which is obviously different from the darker radial veins (Fig. 21) and by the characteristic light brown thorax with three black spots (which may be fused) on the scutum (Fig. 17). At a first glance this species resembles *P. schmidegeri* Stuke, 2017 which occurs in the Arabian Peninsula (Stuke, 2017b) but *P. guillarmodi* is distinguished by the complete dusting band which starts immediately above the middle coxa and reaches up to the notopleuron without becoming narrower. In the event that *P. brevipennis* is eventually demonstrated to be an aberrant and misshaped *antiqua* specimen (see above) this will also be distinguished from *P. guillarmodi* by its dark brown subcosta which does not differ in colour from the radial veins.

### Etymology

This species is named in honour of Charles Frédéric Jacot Guillarmod (1912–1979), who collected several specimens of this new species and whose collecting activities made a huge contribution to knowledge of the Diptera of South Africa.

### Distribution

*Physocephala guillarmodi* is widely distributed in the Afrotropical Region (Fig. 24).

### *P. larvata* (Speiser, 1911)

(Figs 25–29)



*Conops (Physocephala) larvatus* Speiser 1911  
= *Physocephala similis* Kröber 1915 (**syn. nov.**)

**Material.** DEMOCRATIC REPUBLIC OF CONGO: 1♂, 30.xii.1952, Nord-Kivu, Kinshasa, Vitshumbi, s Lake Edward, leg. J. Verbeke, coll. ISNB; TANZANIA: 1♂, 1911, Marienhof [=Murutunguru], Ukerewe, leg. Conrads, coll. SMTD; UGANDA: 1♂, 12.viii.1958, Uganda, det. as *P. similis* by Camras 2000, leg. J. Bowden, coll. NHML [NHMUK010922104].

*Physocephala similis* was distinguished from *P. larvata* by Camras (2001) within his *similis* species-group, but the character which Camras used to identify *similis* (“Face yellow”) contradicts the original description of Kröber (1915). Kröber compared *P. similis* with *P. larvata* and stated that *P. similis* “Ist *P. larvata* zum verwechseln ähnlich, hat aber ganz andere Flügelzeichnung” [Is confused with the similar *P. larvata*, but has quite a different wing pattern] although this difference is not obvious when comparing the original descriptions of *P. similis* and *P. larvata*. Both descriptions fit to the wing shown in Fig. 27 and there remains no other difference between these two species. The depository of the holotype is unknown (Stuke 2017a) and therefore *Physocephala similis* Kröber, 1915 is placed as a junior synonym of *Physocephala [Conops] larvatus* Speiser, 1911 (**syn. nov.**).

***P. ssymanki* spec. nov.**  
(Figs 30–35)

urn:lsid:zoobank.org:act:7476796B-0C67-44D8-AA85-1313BC97B38C

**Holotype** ♂. (1) “98/99/79”; (2) “visiting white fls / *Brownanthus kuntzei* / (Schinz) Ihlenf. & Bittrich / Aizoaceae: Mesembryanthema”; (3) “Namibia / NW of Cape Cross / 21.44S 13.59E / 14.iii.1999 / F. W. and S. K. Gees; (4) Holotypus / *Physocephala ssymanki* / spec. nov. / 2018”. Holotype is deposited in AMGS. The specimen is pinned and in perfect condition.

#### Description of holotype (male)

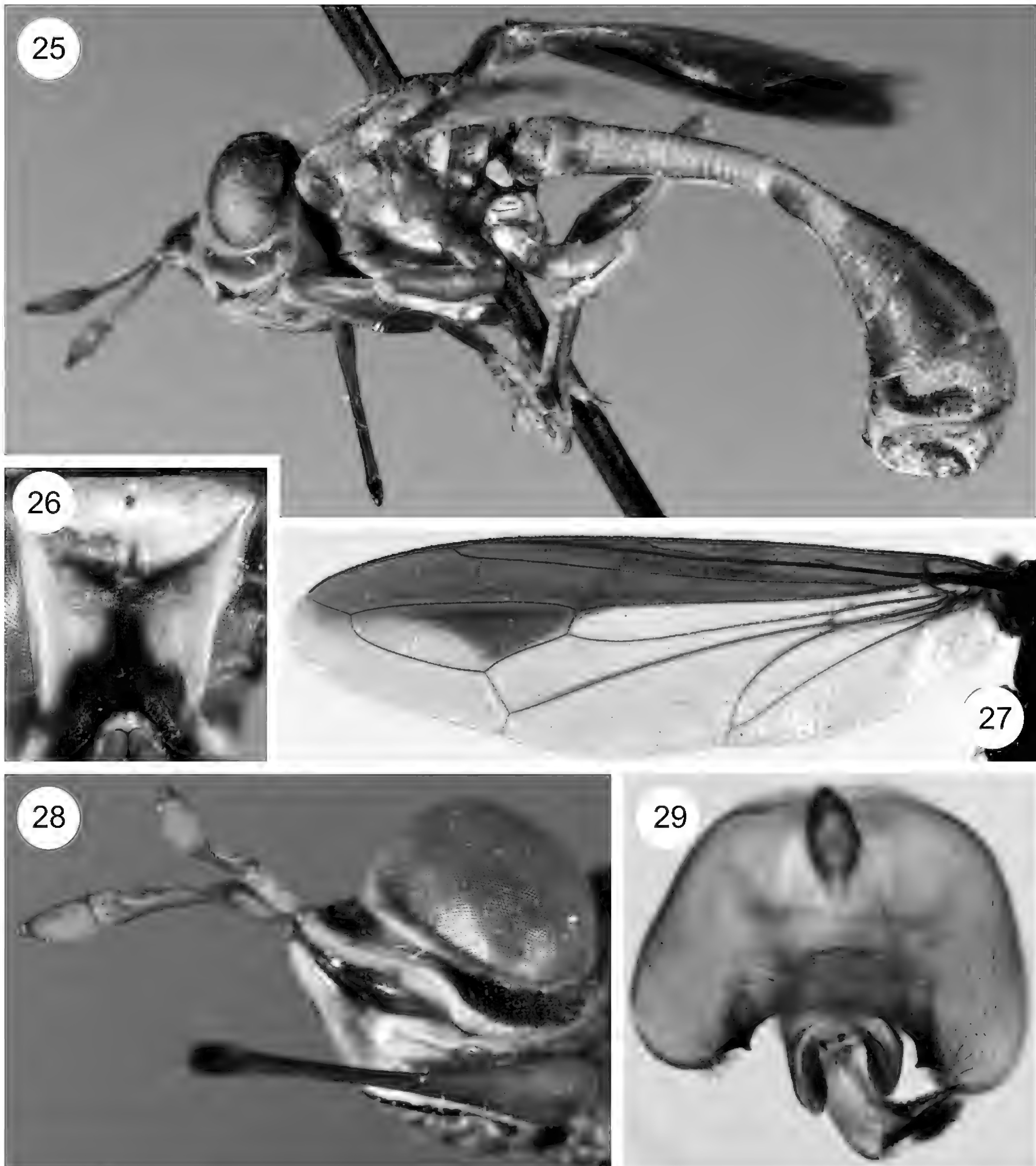
Length 11.7 mm; Wing-length 7.0 mm; Head-height 2.6 mm.

**Head.** Antenna black, tip of pedicel and base of first flagellomere brown. Arista stylus-like, with 2 aristomeres situated at tip of first flagellomere (Fig. 32). Both aristomeres minute, length of apical aristomere shorter than height. Scape about twice as long as maximum width, apically with black setae. Pedicel about six times longer than maximum width, mainly dorsally and apically covered with black setae. Pedicel lacking any ridge at base, and expanded towards apex. First flagellomere long and conical, about 2.5 times as long as high, pointed, ventrally lacking a membranous area. Lunule between base of antennae and ptilinal suture distinct, shorter than width

of scape. Eye brown, lacking ommatrichia, with facets all of about the same size. Posterior margin of eye lacking any shining indentation. Gena height / eye height (measurements taken from head in lateral view) = 0.2. No ocellar tubercle, no ocelli and no ocellar triangle evident. Frons (Fig. 31) broader than long, slightly concave, slightly projecting above eyes posteriorly, and lacking setulae. Anterior margin concave. Frons yellow, with no frontofacial spot and with indistinct dusting all over. Vertex as broad as frons, separated from latter by a more or less distinct ridge. Vertex shining, and in posterior half covered with black setulae; apically with an indistinct depression. Ridge of vertex with minute longitudinal grooves. Face yellow, lacking dusting except for some silver dusting along eye margin. Gena yellow, lacking setae. Distinct facial grooves reaching mouth edge, and facial carina reaching from base of antennae to a distinctly broadened and outstanding frontoclypeal tubercle. Ptilinal suture extending well beneath antennal bases on either side. Oral cavity tapers dorsally. Postcranium not obviously invaginated, black to dark brown. Whole postcranium slightly dusted, with dusting adjacent to posterior margin of eye obviously denser. Occiput and postgena covered with black setulae. Postgena not widened and not delimited from occiput. Bottom portion of postcranium not delimited and not setulose. Proboscis black to reddish-brown, labellum black. Frontoclypeal membrane long, light orange-brown and hardly delimited from orange-brown clypeus. Palps absent. Labium longer than head-length in lateral view, distinctly thickened basally, and with anterior section completely fused into a tube. Labrum not visible in the holotype. Labellum short, completely divided, hardly broader than adjacent haustellum, and covered with very short setulae only.

**Thorax** mainly black, with pleura black to brown. Postpronotum orange-brown. Thorax grey-dusted all over, with distinct dust-stripe reaching from middle coxa to notopleuron and becoming wider dorsally. Anterior half of anepisternum and posterior half of anepimeron shining (Fig. 34). Presternum distinct, broad. Basisternum broad, ventrally narrowed to a point, lacking setae or setulae. Proepisternum lacking setae or setulae. Scutum covered with small black setae. Notopleuron with several stronger setae. Postalar callus with a few strong, short black setae above several curved setulae. Katepisternum with 2 setae posterodorsally and no setae ventrally. Metakatepisternum lacks setae. Anepimeron with 12 long setulae about as long as maximum width of tibiae. Mediotergite convex, with minute and barely visible black setae. Subscutellum inconspicuous. Scutum covered with scattered small black setae, and with no outstanding setae. Wing as Fig. 35: Fore margin of wing tinged brown, with brown membrane between subcosta and radius  $R_{4+5}$ . Cell  $r_{2+3}$  hyaline apically and cell  $r_{4+5}$  brown basally. Veins brown, subcosta paler brown than radial veins. Wing mostly covered with microtrichia, but with basal cell, basal me-



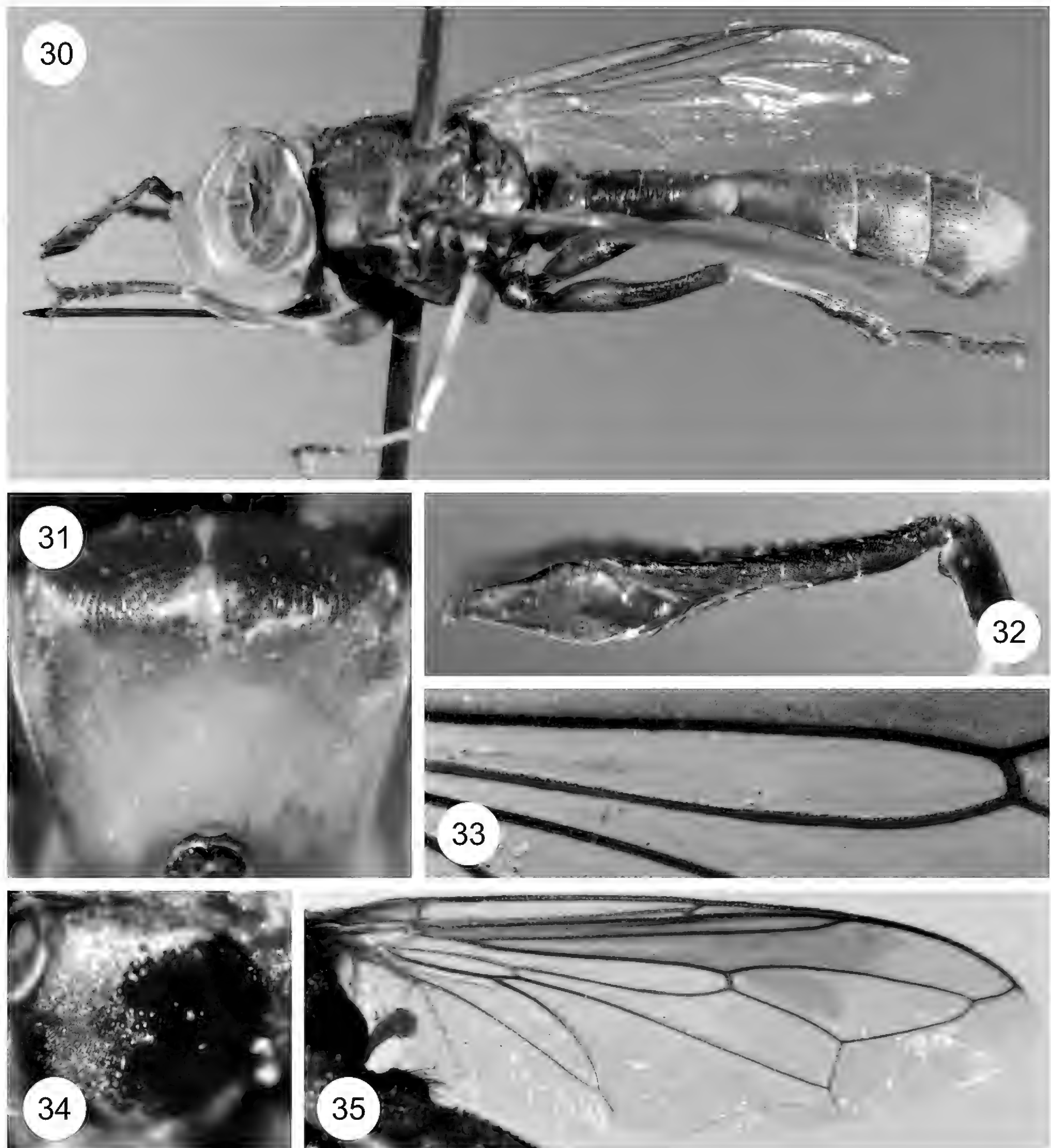


**Figs 25–29.** *Physocephala larvata* (Speiser, 1911). **25.** Habitus, lateral view (♂, Vitshumbi); **26.** Frons, dorsal view (♂, Marienhof); **27.** Wing, dorsal view (♂, Vitshumbi); **28.** Head, ventrolateral view (♂, Marienhof); **29.** Epandrium, dorsal view (♂, Marienhof).

dial cell, base of discal-medial cell and base of cubital cell cup lacking microtrichia. Radial-medial crossvein small but complete. Basal-medial-cubital crossvein also complete. Radius  $R_1$  and  $R_{2+3}$  terminate close together in costa, well beyond insertion point of subcosta in costa.

Radius  $R_{4+5}$  with shallow and even curve in distal section directed towards fore-edge of wing. Cell  $r_{4+5}$  pedunculate, with vein  $R_{4+5}+M_1$  well expressed and distinctly longer than radial-medial crossvein. Basal cell lacks any thickening. Cubital cell cup elongated, distinctly longer than





**Figs 30–35.** *Physocephala ssymanki* spec. nov. (holotype). **30.** Habitus, lateral view; **31.** Frons, dorsal view; **32.** Antenna, lateral view; **33.** Basal cell, dorsal view; **34.** Anepisternum, dorsolateral view; **35.** Wing, dorsal view.

vein  $A_1+CuA_2$ , and pointed distally (i.e. cubitus  $CuA_2$  and anal vein  $A_1$  meet at an acute angle). Vein  $A_1+CuA_2$  not reaching hind margin of wing. Cubital veins  $CuA_1$  and crossvein distinctly separated. Upper and lower calypters yellowish-white to brown, margin of upper calypter

with white setulae. Alula almost square, about as long as broad, lacking setulae on posterior margin. Venae spuriae pronounced in cell  $r_{4+5}$  and cubital cell cup. Haltere white, with light brown base. Knob of haltere with brown setulae. Legs orange, with hind femur and hind tibia black



in apical half. Legs with inconspicuous silver dusting or shining, hind coxa densely silver-dusted. Posterior surfaces of fore and middle tibiae with obvious silver-dusted fields distally. Legs generally with short, adpressed black setulae. Base of fore and middle femora basally with denser black setulae. Areas of dense black to brown setulae anteroventrally on tip of fore tibia and ventrally and posteriorly at tip of hind tibia. Middle femur lacking any distinct row of regularly arranged setulae. Hind femur lacking outstanding setulae. No preapical setae dorsally, and no setae ventrally on tibiae. Femora ventrally lacking rows of short black setae. Coxae with several setae, but lacking any outstandingly long ones. Hind femur slightly thickened in basal half. All tibiae thickened in apical half. Each metatarsus with 0–1 stronger seta ventrally at base. Pulvilli yellowish-white. Claws brown, with broad black tips. Empodium light brown, and about as long as pulvilli.

**Abdomen** orange to dark brown, with diffuse paler markings. Abdomen with short black setulae all over. ♂ abdomen strongly dusted from posterior half of tergite 3 to tip (in anterior view) and almost shining laterally on tergites 1–3. No obvious dusting at hind margin of tergites. Tergites 1–3 fused but remain distinct. Abdomen of holotype not dissected. Tergite 1 with obvious black setulae on bulbous lateral projections. Tergite 2 elongated, about four times as long as smallest width, lacking obvious lateral tufts of setulae. Tergite 3 slightly widened posteriorly, about twice as wide posteriorly than anteriorly. Tergite 5 and sternite 5 separate. Sternite 5 with scattered long black setulae and denser small black setulae forming an indistinct field. Protandrium broader than epandrium and projecting over it. Sternite 8 distinctly delimited from protandrium. Indistinct line of small black setulae at border between sternite 8 and protandrium. Paired cerci distinct, completely sclerotised and covered with scattered setulae. Epandrium not fused behind cerci, but with a slightly sclerotised connection at both sides of epandrium.

### Diagnosis

*Physocephala ssymanki* belongs to the *P. antiqua* species-group and can easily be recognised from the anepimeron, which has several characteristically long setulae which are about as long as the maximum width of the tibiae. The dusting stripe on the pleura obviously contrasts with the shining anepisternum and anepimeron, and becomes wider dorsally (Fig. 34). The hind tibia and femur are black in the apical two-thirds, contrasting with the remaining orange-brown legs (Fig. 30).

### Etymology

This species is dedicated to Axel Ssymank (Bonn) who generously loaned numerous Conopidae specimens for this project.

### Distribution

To date *P. ssymanki* is only known from the locus typicus on the coast of southern Namibia.

### *P. pusilla* (Meigen, 1804)

(Fig. 36)

*Conops pusilla* Meigen 1804

**Material.** CENTRAL AFRICAN REPUBLIC: 1♂ 2♀♀, 4.xii.2010, 60 km w Banibo [3°50'N 16°44'E], 630 m, leg. J. Halada, coll. CULSP.

Afrotropical specimens of this otherwise Palaearctic species have previously caused confusion, and for a long time were suspected of belonging to a different species. Somewhat surprisingly, however, their morphological characters fall within the variability of *P. pusilla* as recently defined by Stuke (2016). *Physocephala pusilla* had not previously been recorded from the Afrotropical Region and was assumed to be a Palaearctic species (Stuke 2017a). Together with *P. antiqua*, *P. vittata* and *Conops elegans* Meigen, 1804, this is the fourth example of a very variable and mainly Palaearctic species with a distribution which extends into the Afrotropical Region.

### *Physocephala bimarginipennis* species-group

Only one distinct Afrotropical species is included in this group, as was also recognised by Camras (2001). *Physocephala bimarginipennis* was previously treated in the genus *Archiphysocephala* Kröber 1939, now synonymised. Identification using the characters given in Key 1 is straightforward.

### *P. bimarginipennis* Karsch, 1887

(Figs 37–41)

*Physocephala bimarginipennis* Karsch 1887

= *Physocephala gigantea* Kröber, 1936

**Primary type material examined.** ♀ holotype of *Physocephala bimarginipennis* Karsch, 1887: (1) “Pungo Andongo / A. v. Homayer”; (2) “11031”; (3) “*Physocephala / bimarginipennis* / n. sp.”; (4) “Holotypus”; coll. ZMHB.

♂ syntype of *Physocephala gigantea* Kröber, 1936: (1) “Ph. Type / *gigantea*”; (2) “Musée du Congo / Elisabethville / XI-1927 / Dr. M. Bequaert”; (3) “*Physocephala / gigantea* / Krb. / det. Kröber 1935”; (4) “R. DET / V / 2992”; (5) “Typus”; (6) “RMCA ENT / 000012173”; coll. MRAC.

♂ syntype of *Physocephala gigantea* Kröber, 1936: (1) “Paratype / Ph. *gigantea*”; (2) “Musée du Congo / Kivu: Musingiro / 8-IX-1927 / Ch. Seydel”; (3) “Musingiro [si] / 8 Sept. 1927 / Ch. Seydel”; (4) “*Physocephala / gigantea* Krb. / det. Kröber 1935”; (5) “R. DET / W / 2992”; coll. MRAC.





Fig. 36. Habitus of *Physocephala pusilla* (Meigen, 1804) (♂, w Banibo).

**Additional material.** DEMOCRATIC REPUBLIC OF CONGO: 1♀, 8.vii.1937, Bambesa, det. as *P. gigantea* by Janssens 1954, leg. J. Vrydagh, coll. MRAC; 1♀, vi.1932, Eala, det. as *P. bimarginipennis* by Camras 1962, leg. A. Corbisier, coll. MRAC; 1♀, 5.iii.1954, North Kivu Province, Lac Vert, forêt route Goma – Sake, leg. J. Verbeke, coll. ISNB; ETHIOPIA: 1♀, 4.xii.2014, Bonga Waldsaum, 1628 m [07°11.87'N 036°15.13'E], *Bothriocline schimperi*, leg. H.-J. Flügel, coll. PHJF; 1♂, viii.2019, Bonga, Kafa Development Association Guesthouse [7°14'59.14"N 36°15'12.26"E], leg. T. Kirsche, coll. PJHS; KENYA: 1♀, 16.xi.1967, Nairobi, ex *Xylocopa flavorufa* found dead 23.ix.1967 Green Office Colony, [collector unknown], coll. NHML; 1♀, 9.–23.v.2006, Coast Province, Shimba Hills National Park, near artificial Ponds [4.22752°S 39.43197°E], 335 m, mixed grass-shrub-land, Malaise trap, leg. R. Copeland, coll. NMKE; SOUTH AFRICA: 1♀, 1.–3.iv.2001, Mpumalanga Province, Blyderevierspoort NP [24°39'S 30°50'E], leg. D. J. Greathead, coll. ZMHB; TOGO: 1♂, ii.2017, Kloto, forest area [6°57'31.66"N 0°34'29.75"E], leg. G. Goergen, coll. IITA; 1♀, xii.2016, ditto; 1♀, x.2001, ditto; UGANDA: 1♂, 22.vii.1966, Kwanda, ex ♂ *Xylocopa rufa*, leg. D. J. Greathead, coll. NHML; 1♀, 12.iii.2012, Western Uganda, n Fort Portal Kijura, forest edge [N302540 E004731], leg. Oehlke, coll. PASS.

#### *Physocephala caenoneura* species-group

Species belonging to this group were previously included together with other species in the *Pseudophysocephala nigritarsis* species-group of Camras (2001). This caused some confusion because these species may have both a distinct vena spuria which is well separated from radius

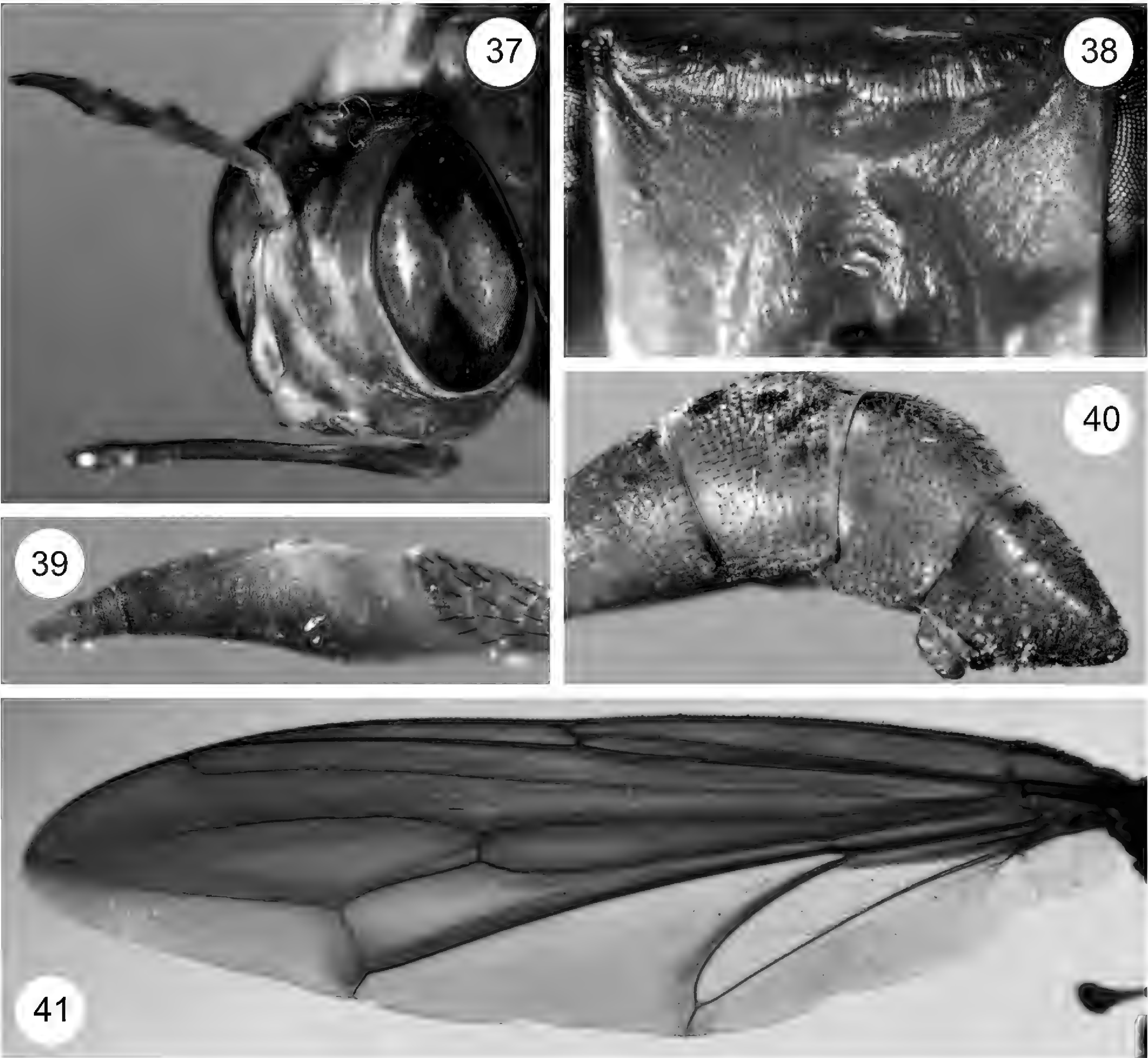
$R_{4+5}$ , and short apical abdominal segments, thus potentially appearing to fall within his *Pseudophysocephala vitripennis* and *Pseudophysocephala platycephala* species-groups respectively.

Females of the *caenoneura* species-group are easily recognised by the normally developed, usually adpressed theca and short tergites 5 and 6. From outside the *caenoneura* group, only *P. microvena* and *P. pseudomicrovena* share this combination of characters but are easily recognised as belonging to the *Physocephala microvena* species-group by the lack of a vena spuria in cell  $r_{4+5}$ , and typically also by the reduced or absent radial-medial crossvein. Males of *caenoneura* group can be more difficult to assign, however, the elongated basal aristomere and less modified wing venation being the only characters which reliably distinguish them from males of the *microvena* species-group. All members of this group are restricted to the Afrotropical Region.

#### Key 4 – Identification of the *Physocephala caenoneura* species-group

1. Basal cell completely hyaline and almost completely lacking microtrichia, or with only very short microtrichia which are hardly visible and much less obvious than those on the remaining wing (e.g. Fig. 53); base of cell  $r_{2+3}$  hyaline; hind femur at most with an indistinct dark spot ..... 2
- Basal cell at least with some dark colouration and sometimes completely black or brown, and almost completely covered with microtrichia similar to those on the remainder of the wing (e.g. Fig. 59); cell  $r_{2+3}$  completely brownish infuscated (e.g. Fig. 59); hind femur may have a distinct blackish ring





**Figs 37–41.** *Physocephala bimarginipennis* Karsch, 1887 (♂, Kawanda). **37.** Face, frontal view; **38.** Frons, dorsal view; **39.** Arista, lateral view; **40.** Tip of ♂ abdomen, lateral view; **41.** Wing, dorsal view.

- which is sharply demarcated from the orange-brown colouration..... **3**
- 2.** Tarsi orange-brown, not contrasting with tibiae; apical aristomere typically less than half length of projection on basal aristomere (Fig. 48); antennae completely orange-brown (Fig. 47); gena usually brownish, contrasting with yellow face (Fig. 47); ♀ theca short in side view, distinctly shorter than wide ..... *P. braunsi* (Kröber, 1931)
- Tarsi dark brown, contrasting with brown tibiae (Fig. 51); apical aristomere more than half as long as projection on basal aristomere (Fig. 50); antennae black to brown, with a contrasting orange-brown scape (sometimes faded in old specimens) (Fig. 50); gena usually yellow, like the face; ♀ theca long, almost as long as wide (Fig. 54)..... *P. caenoneura* Kröber, 1939
- 3.** Projection of basal aristomere elongated, about twice as long as apical aristomere (Fig. 58); radial veins dark brown (Fig. 59); basal cell only slightly darkened, obviously paler than cell  $r_{2+3}$  (Fig. 59) ..... *P. capensis* Kröber, 1931
- Projection of basal aristomere not as elongated, not much longer than apical aristomere (e.g. Figs 44, 61, 65); radial veins sometimes light orange-brown; basal cell mostly as dark as cell  $r_{2+3}$  (e.g. Fig.



45); base of cell  $r_{4+5}$  and usually apex of basal cell hyaline, and therefore radial-medial crossvein within a hyaline patch (e.g. Fig. 60)..... 4

4. Characteristic dark mark at junction of discal medial-cubital crossvein and media (Fig. 60); ♀ theca obviously short, with about 7 interrupted rows of black setae. .... ***P. fenestralis* (Kröber, 1939)**
  - Wing colouration different, lacking dark mark at junction of discal medial-cubital crossvein and media, nor with hyaline spot surrounding radial-medial crossvein; ♀ theca longer, with more than 15 interrupted rows of black setae (e.g. Figs 43, 64) ... 5
5. At least base of media and subcosta light yellowish-brown; scutum orange-brown, with three elongated blackish spots (Fig. 63); katapisternum orange-brown; ♀ with black setulae on theca less dense, not obscuring underlying surface (Fig. 64).....
  - ..... ***P. rufitarsis* (Camras, 1962)**
    - Veins uniformly dark brown; scutum mainly blackish, with no distinct spots (Fig. 42); katapisternum mainly black; ♀ with black setulae on theca denser, largely obscuring underlying surface (Fig. 43).....
      - ..... ***P. afenestralis* (Camras, 2001)**

***P. afenestralis* (Camras, 2001)**

(Figs 42–45)

*Pseudophysocephala afenestralis* Camras 2001

**Material.** SOUTH AFRICA: 1♀, 20.–24.xi.2014, KwaZulu-Natal Province, Royal Natal National Park, Gudu Bush falls [28°40.925'S 28°55.778'E], 1628 m, Malaise trap in indigenous afro-montane forest, leg. A. H. Kirk-Spriggs & E. Letsobe, coll. BMSA.

***P. braunsi* (Kröber, 1931)**

(Figs 46–49)

*Physocephala braunsi* Kröber 1931

**Material.** SOUTH AFRICA: 1♂, 15.iv.1948, Marieps Mountain, det. as *P. braunsi* by Camras 2000, leg. G. van Son., coll. FMNH; 1♂, xi.1933, Cape Province, Swellendam, det. as *P. platycephala* by Kröber 1938, det. as *P. braunsi* by Camras 2000, leg. R. E. Turner, coll. NHML [NHMUK010922151]; ZIMBABWE: 1♀, 7.xii.1976, Salisbury [= Harare] [17.84 31.05], leg. P. E. Hulley, coll. AMGS.

We are not convinced that the characters used to distinguish *P. braunsi* from the very similar *P. caenoneura* merit separate species status, but the few specimens which are available can be segregated using the characters given in Key 4.

***P. caenoneura* (Kröber, 1939)**

(Figs 50–54)

*Pseudophysocephala caenoneura* Kröber 1939

= *Pseudophysocephala stylata* Kröber 1939

**Primary type material examined.** ♀ holotype of *Pseudophysocephala caenoneura* Kröber 1939: (1) “Type”; (2) “Nyassa-See / Langenburg / 26.VII.–8.VIII. 98 / Fülleborn S.”; (3) “Typus”; (4) “*Pseudophysocephala / stylata* Kb. / det. Kröber 1938”; (5) “Zool. Mus. / Berlin”; coll. ZMHB.

1 ♂ holotype of *Pseudophysocephala stylata* Kröber 1939: (1) “Type”; (2) “Nyassa-See / Langenburg / 1.–26.VII.98 / Fülleborn S.”; (3) “Typus”; (4) “*Pseudophysocephala / stylata* Krb.”; (5) “Zool. Mus. / Berlin”; (6) “*Pseudophysocephala / caenoneura* Kröber / det. Camras 1999”; coll. ZMHB.

**Additional material.** KENYA: 1♀, 2.iii.1993, Ilrad, w Nairobi, 1900 m, leg. B. Merz, coll. TAU; 1♀, 10.viii.2004, near Karura Forest, Nairobi [1°14.829'S 36°48.953'E], leg. R. Copeland, coll. NMKE; TANZANIA: 1♂ 1♀, 4.ii.1977, Amani, East Usambara, 1000 m, det. as *P. caenoneura* by Camras 1999, leg. H. Enghoff, O. Lomholdt, O. Martin, coll. FMNH; 1♂, 10.iii.1963, Kilimajaru, Weruweru, det. as *P. caenoneura* by Camras 1999, leg. D. J. Greathead, coll. NHML [NHMUK010922144]; 1♂, 20.iv.1966, plains e Arusha, det. as *P. caenoneura* by Camras 1999, leg. D. J. Greathead, coll. NHML [NHMUK010922145]6.

***P. capensis* Kröber, 1931**

(Figs 55–59)

*Physocephala capensis* Kröber 1931

**Material.** SOUTH AFRICA: 1♂, 25.ii.2016, Barberton, Mpumalanga [25°10'18"S 30°56'45"E], 1400 m, leg. A. Ssymank, coll. PASS; 1♀, 4.–7.xi.1931, Cape Province, George, det. as *P. capensis* by Kröber, leg. H. P. Thommaset, coll. NHML [NHMUK010922135]; 1♀, 23.ix.2007, Eastern Cape Province, Zuurborg [33°21'S 25°44'E], leg. C. Turnbull, coll. AMGS; 1♀, 15.xii.2012, KwaZulu-Natal Province, Kwela Lodge, Pietermaritzburg [29°29'34"S 30°21'40"E], 930 m, leg. G. Ståhls, coll. PASS; 1♂, 15.x.2003, Western Cape Province, Humansdorp [34°1'60S 24°46'0E], 114 m, leg. C. Hepburn, coll. AMGS.

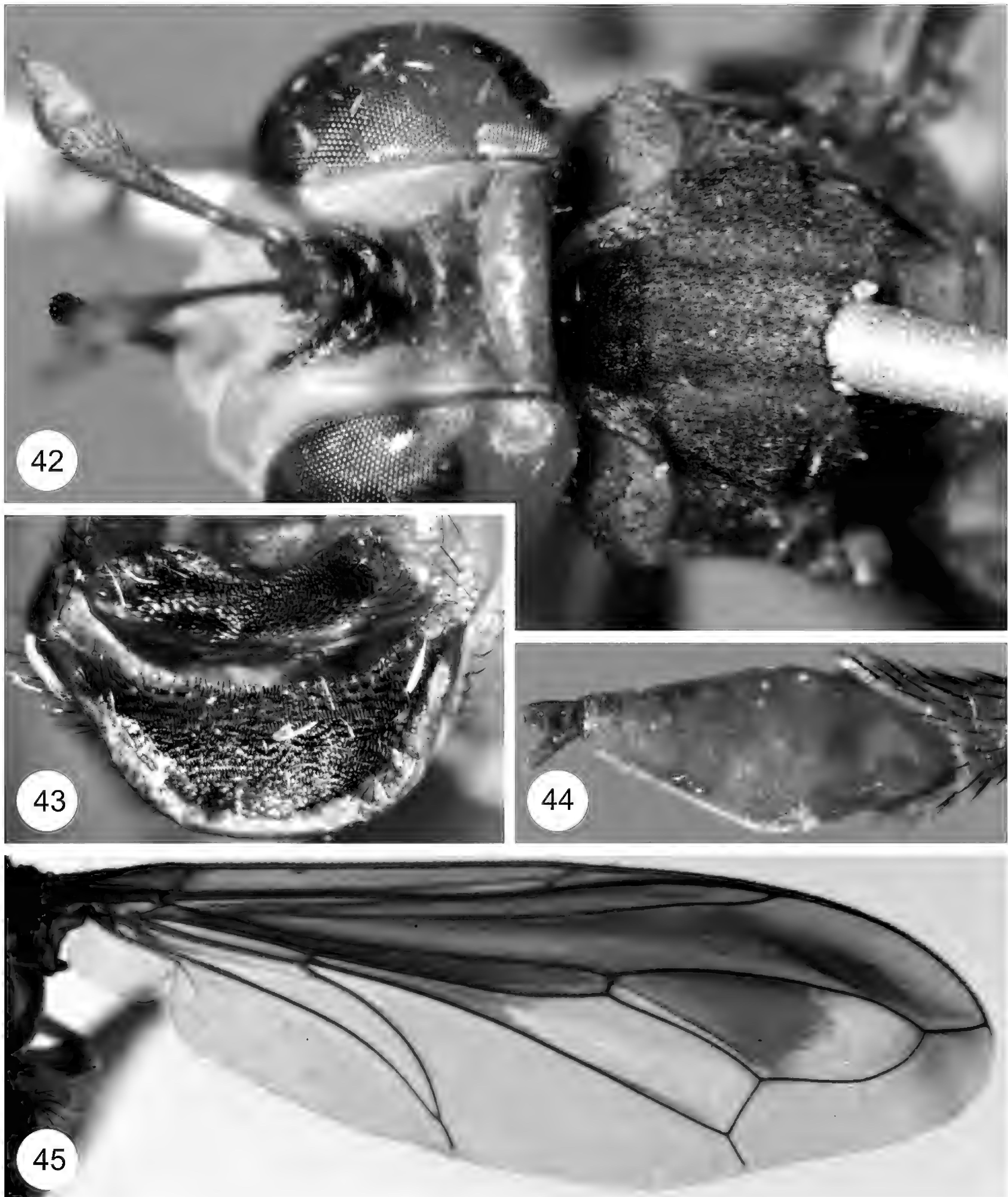
***P. fenestralis* (Kröber, 1939)**

(Figs 60–62)

*Pseudophysocephala fenestralis* Kröber 1939

**Primary type material examined.** 1 ♂ syntype of *Pseudophysocephala fenestralis* Kröber 1939: (1) “Type”; (2) “Nyassa-See / Langenburg / 14.V.1999 / Fülleborn S.”; (3) “Typus”; (4) “*Pseudophysocephala*”



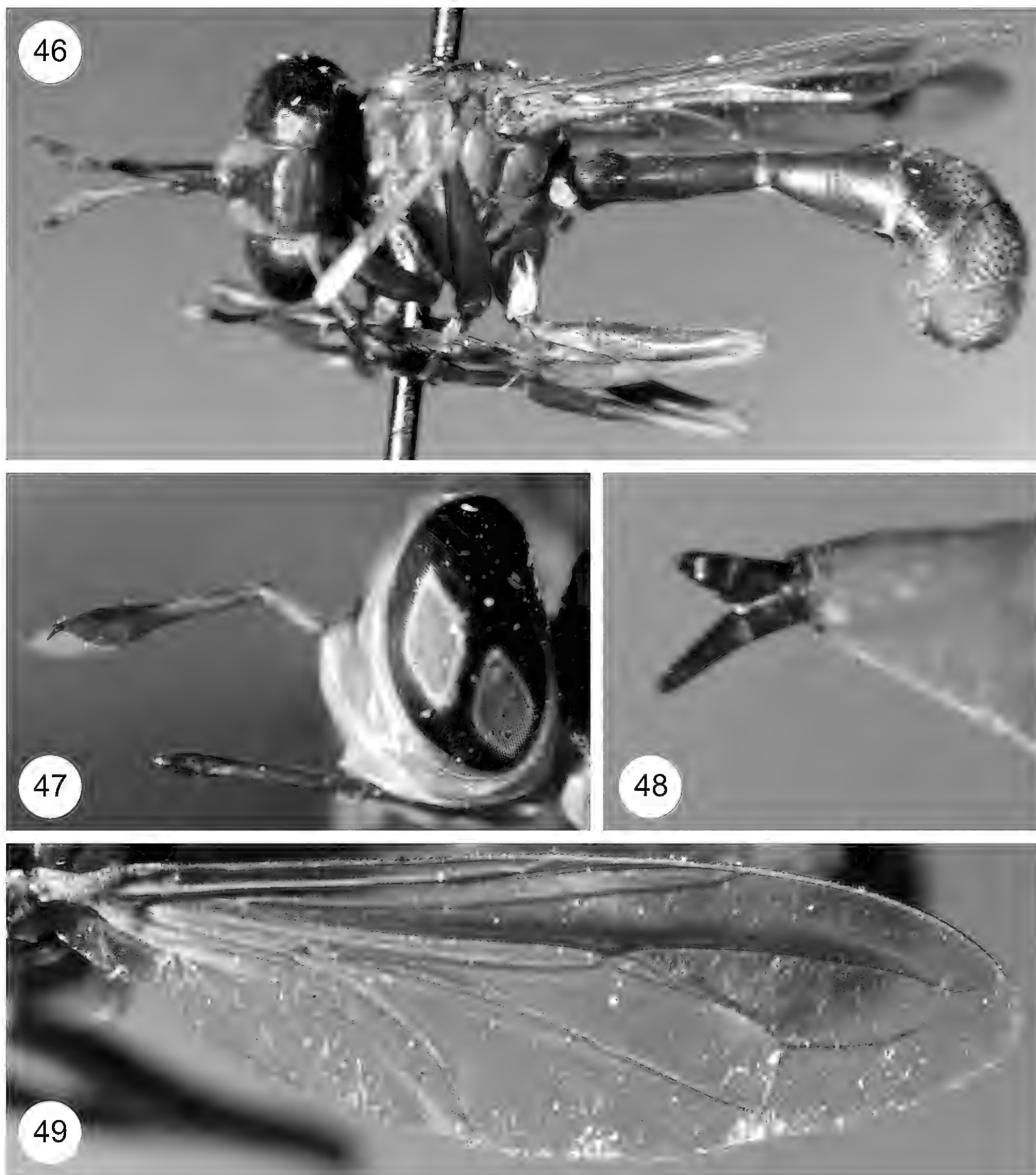


**Figs 42–45.** *Physocephala afenestralis* (Camras, 2001) (♀, Royal Natal National park). **42.** Frons and scutum, anterodorsal view; **43.** Theca, ventral view; **44.** Arista, lateral view; **45.** Wing, dorsal view.

*la / fenestralis* Krb. /det. Kröber 1938”; coll. ZMHB.

1♀ syntype of *Pseudophysocephala fenestralis* Kröber 1939: (1) “Syn- / type”; (2) “George, Cape Province, / 27.VI.–1.VII.1920.”; (3) “S. Africa / R. E. Turner. / 1920-



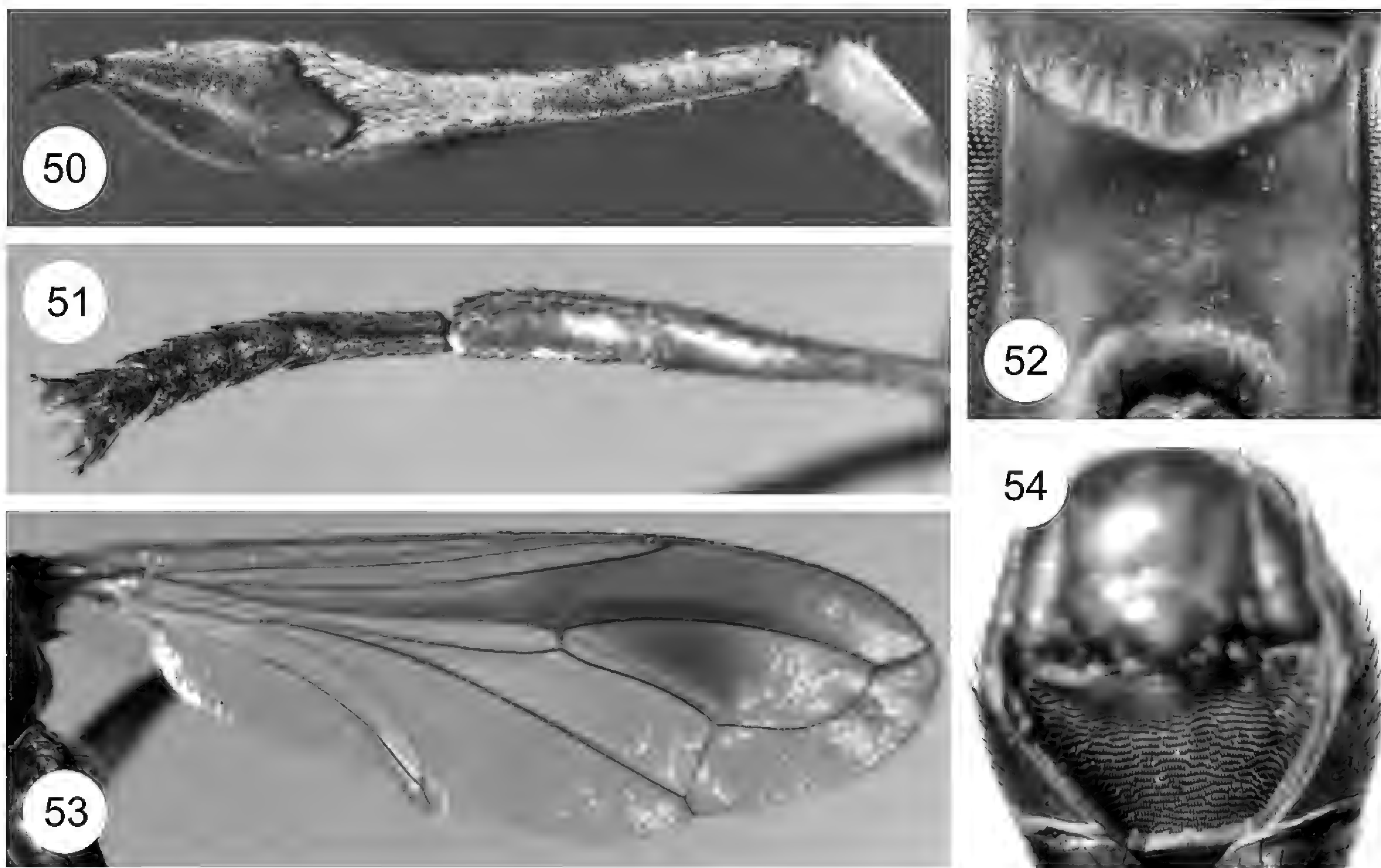


**Figs 46–49.** *Physocephala braunsi* Kröber, 2001 (♂, Marieps Mnt.). **46.** Habitus, lateral view; **47.** Head, lateral view; **48.** Arista, lateral view; **49.** Wing, ventral view.

318.”; (4) “*Pseudophysocephala fenestralis*, Krb. / examined & det. / O. Kröber, 1938.”; (5) “*Pseudophysocephala fenestralis* / Krb”; coll. NHML.

**Additional material.** TANZANIA: 1♀, 20.viii.1980, Mt. Rungwe, sw, 1900 m, det. as *P. fenestralis* by Camras 2000, leg. M. Stoltze, N. Scharff, coll. FMNH; 1♀, 16.ii.1952, Njombe, 6000–6500 ft, det. as *P. fenest-*





**Figs 50–54.** *Physocephala caenoneura* (Kröber, 1939) (♀, Nairobi). **50.** Antenna, lateral view; **51.** Leg with tarsi, dorsal view; **52.** Frons, dorsal view; **53.** Wing, dorsal view; **54.** Theca, posterior view.

*tralis* by Camras 1999, leg. W. Peters, coll. NHML [NHMUK010922142].

***P. rufitarsis* (Camras, 1962)**

(Figs 63–65)

*Pseudophysocephala rufitarsis* Camras 1962

**Primary type material examined.** ♀ holotype of *Pseudophysocephala rufitarsis* Camras 1962: (1) “Holo- / type”; (2) “S. Africa. / R. E. Turner / Brit. Mus. / 1933-108.”; (3) “Holotype ♀ / *Pseudophysocephala* / *rufitarsis* / Camras”; (4) “*Pseudophysocephala* / *platycephala* Loew / examined & det. / O. Kröber. 1938”; (5) “E. Cape Prov. / Katberg. / 15–30.i.1933.”; (6) “BMNH(E)# / 249149”; coll. NHML

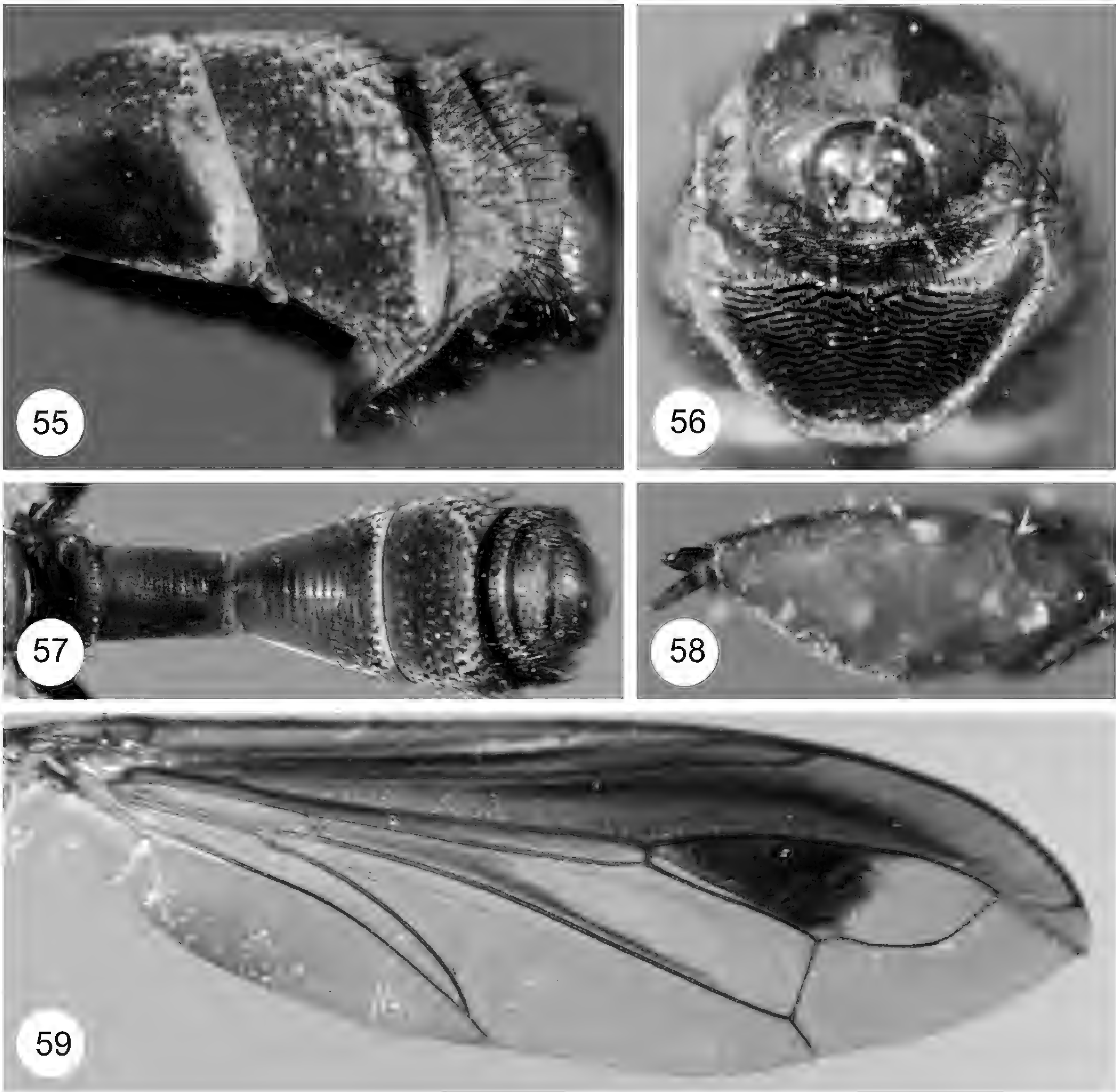
**Additional material.** SOUTH AFRICA: 1♂, i.1953, Natal, Hilton Road, det. as *P. rufitarsis* by Camras 2000, leg. P. Graham, coll. NHML [NHMUK010922159]; 1♂, xi.1930, Cape Province, Somerset East, det. as *P. platycephala* by Kröber 1938, det. as *P. rufitarsis* by Camras 2000, leg. R. E. Turner, coll. NHML [NHMUK010922162]; 2♂♂, 19.x.1994, Cape Province, Tsitsikama National Park, Storms River Pass [33°59'S 23°55'E], leg. R. Danielsson, coll. MZLU; 1♀, 1.–10.1932, Eastern Cape Province, Katberg, det. as *P. platycephala* by Kröber 1938;

det. as *P. rufitarsis* by Camras, 2000, leg. R. E. Turner, coll. NHML [NHMUK010922189]; 1♀, 1.–10.1932, Eastern Cape Province, Katberg, det. as *P. platycephala* by Kröber 1938; det. as *P. rufitarsis* by Camras, 2000, leg. R. E. Turner, coll. NHML [NHMUK010922190]; 1♂, 11.–18.ii.1933, Eastern Cape Province, Katberg, det. as *P. platycephala* by Kröber, 1938, det. as *P. rufitarsis* by Camras 2000, leg. R. E. Turner, coll. NHML [NHMUK010922158]; 1♂, 1.–10.ii.1933, Eastern Cape Province, Katberg, det. as *P. platycephala* by Kröber 1938, det. as *P. rufitarsis* by Camras 2000, leg. R. E. Turner, coll. NHML [NHMUK010922160]; 1♂, 1.–12.iii.1933, Eastern Cape Province, Katberg, det. as *P. platycephala* by Kröber 1938, det. as *P. rufitarsis* by Camras 2000, leg. R. E. Turner, coll. NHML [NHMUK010922161]; 1♀, 15.–30.i.1933, Eastern Cape Province, Ratberg, det. as *P. platycephala* by Kröber 1938, det. as *P. rufitarsis* by Camras 2000, leg. R. E. Turner, coll. FMNH.

***Physocephala halterata* species-group**

Camras (1962b) originally placed *P. congoensis* and *P. halterata* in his *Physocephala halterata* species-group and *P. acroschista* – very probably misidentified – in his *Pseudophysocephala vitripennis* group. This species-group is easily recognised by the velvety black





**Figs 55–59.** *Physocephala capensis* Kröber, 1931. **55.** Theca, lateral view (♀, Zuurberg); **56.** Theca, posterior view (♀, Zuurberg); **57.** ♀ abdomen, dorsal view (♀, Zuurberg); **58.** Arista, lateral view (♀, Zuurberg); **59.** Wing, dorsal view (♀, Kwela lodge).

halteres. Members of the *Physocephala halterata* species-group can be identified using Key 5 below. All members of this species-group are restricted to the Afrotropical Region.

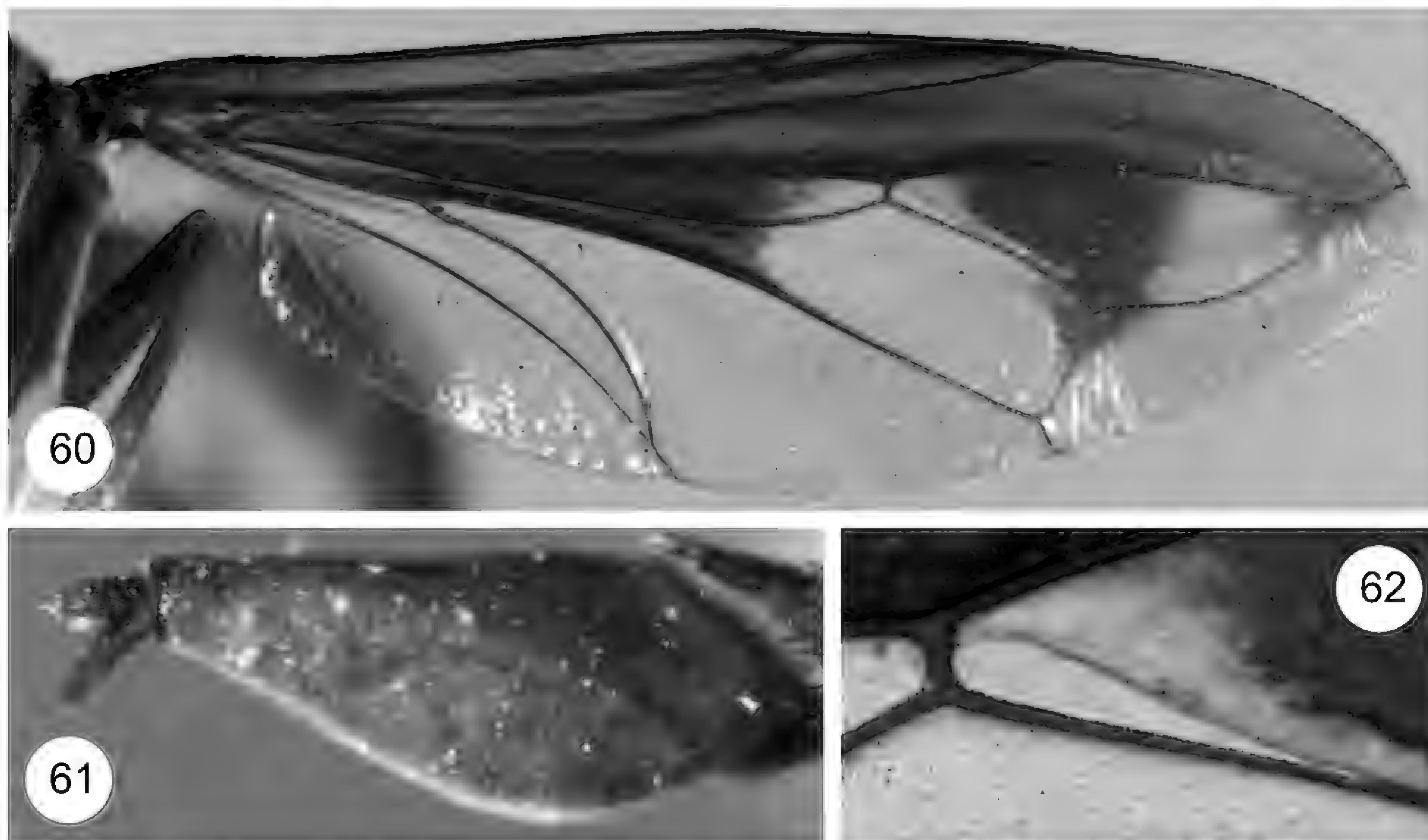
**Key 5 – Identification of the *Physocephala halterata* species-group**

1. Frons orange-brown, lacking any distinct blackish marking (Fig. 68); gena and facial groove orange to

black (Fig. 67); at least postpronotum orange-brown; femora orange-brown.... ***P. halterata* Brunetti, 1925**  
– Frons with obvious blackish marking, or completely black (e.g. Fig. 66); gena and facial groove more or less black (e.g. Fig. 66); thorax including postpronotum black to dark brown; femora black .. **2**

2. Frons almost completely black (Fig. 66); gena brown to black..... ***P. congoensis* Kröber, 1936**





**Figs 60–62.** *Physocephala fenestralis* (Kröber, 1939) (holotype). **60.** Wing, dorsal view; **61.** Arista, lateral view; **62.** Wing, venula spuria in cell  $r_{4+5}$ , lateral view.

- Frons black in basal half, and with a black medial line reaching the lunule; gena yellow, with small brown markings.....*P. acroschista* (Speiser, 1911)

***P. acroschista* (Speiser, 1911)**

*Conops (Physocephala) acroschistus* Speiser 1911

**Primary type material examined.** ♂ holotype of *Conops acroschista* Speiser, 1911: (1) “Holo- / TYPE”; (2) “Musée du Congo / Kasai: Kondué / E. Luja”; (3) “R. DÉT / B / 1477”; (4) “Type! / *Conops (Physocephala) acroschistus* m. / P. Speiser det.”; (5) “RMCA ENT / 000012172”; coll. MRAC.

The holotype reported here fits in all aspects to the original description and there is no reason to assume that it is not the type specimen, although according to the original description this should be in the Museum d’Histoire Naturelle du Grand-Duché de Luxembourg (MGDL). Camras (2001) reported concerning a specimen in the MGDL as follows: “The unidentified holotype of *acroschista* was finally found by J. M. Guinet and he informed me that Luja was the collector.” The specimen reported by Camras (2001) was a female, however, whereas in the original description it was explicitly stated that the type was a male, and a male is described. Evidently there are more than one specimen bearing the same labels, which

led to the misinterpretation of the female specimen in the MGDL. Camras placed the species in his *Pseudophysocephala vitripennis* species-group, having presumably misinterpreted the species due to this wrongly labelled specimen. The synonymy of *P. intermedia* Kröber, 1936 and *P. acroschista* which was introduced by Camras (2001) is therefore invalid and *P. acroschista* should be treated as valid species (**status rev.: valid species**).

***P. congoensis* Kröber, 1936**

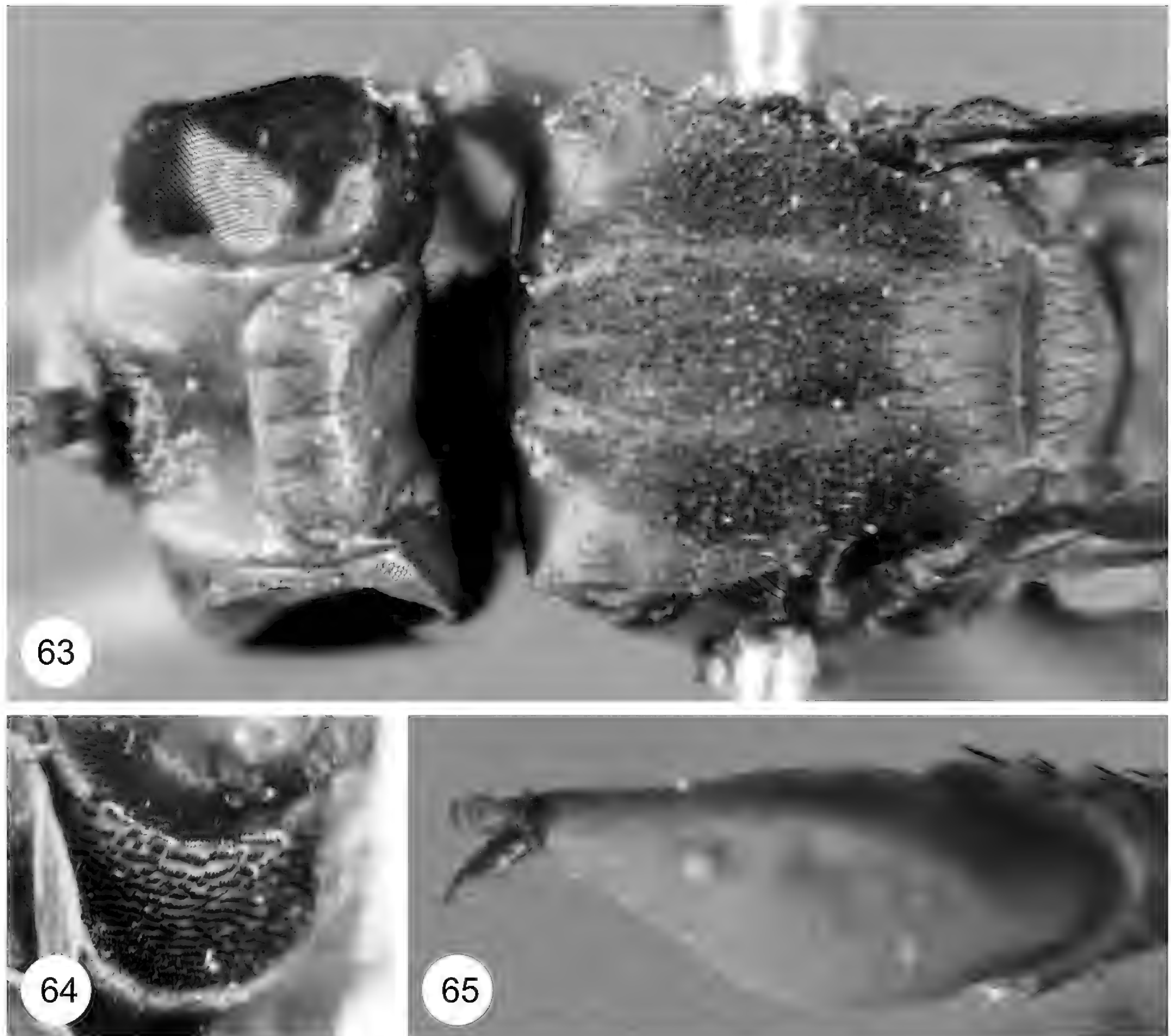
(Fig. 66)

*Physocephala halterata* Brun. var. *congoensis* Kröber 1936

**Primary type material examined.** ♂ syntype of *Physocephala halterata* Brun. var. *congoensis* Kröber, 1936: (1) “Ph. Type ♂ / *halterata* var / *congoensis*”; (2) “Musée du Congo / Bambesa / 15-IX-1933 / H. J. Bredo”; (3) “*Physocephala* ♂ / *halterata* Brun. / var. *congoensis* / Krb / det. Kröber 1935”; (4) “R. DÉT” / P / 2992”; (5) “Typus”; (6) “RMCA ENT / 000012174”; coll. MRAC.

♀ syntype of *Physocephala halterata* Brun. var. *congoensis* Kröber, 1936: (1) “Ph. Type ♀ / *halterata* var / *congoensis*”; (2) “Musée du Congo / Bambesa / 25-IX-1933 / H. J. Bredo”; (3) “*Physocephala* ♀ / *halterata* Brun. / v. *congoensis* Krb / det. Kröber 1935”; (4) “R. DÉT” / Q / 2992”; (5) “Typus”; coll. MRAC.





**Figs 63–65.** *Physocephala rufitarsis* (Camras, 1962) (♀, Katberg). **63.** Head and scutum, dorsal view; **64.** Theca, posterior view; **65.** Antenna, lateral view.

**Additional material.** BURUNDI: 1♂ 1♀, 15.i.1950, Bururi, 1900 m, leg. F. J. François, coll. ISNB; 1♀, 26.v.1949, Bururi Province, Bururi, 1950 m, leg. F. J. François, coll. ISNB; 1♂, 15.v.1949, Bururi Province, Bururi, 2050 m, leg. F. J. François, coll. ISNB; DEMOCRATIC REPUBLIC OF CONGO: 1♀, 21.–27. viii.1931, Tshibinda [–0.287 28.776], det. as *P. congoensis* by Camras 2000, leg. J. Ogilvie, coll. NHML [NHMUK010922105]; 1♂, 5.ii.1949, North Kivu Province, Gishari, Territory Masisi, 2300 m, leg. F. J. François, coll. ISNB; EQUATORIAL GUINEA: 1♀, 15.–31.i.1907, Uelleburg, Benitogebiet, det. as *P. congoensis* by Camras 2000, leg. G. Tessmann, coll. ZMHB.

*Physocephala congoensis* is very similar to *P. halterata* and *P. acroschista*, and all three species could be interpreted as colour morphs of a single species. As Camras (2001) pointed out before, however, the few specimens which are available can be consistently segregated using the characters given in Key 5.

***P. halterata* Brunetti, 1925**

(Figs 67–70)

*Physocephala halterata* Brunetti 1925

**Primary type material examined.** ♀ holotype of *Physocephala halterata* Brunetti 1925: (1) “Holo- / type”; (2) “S. Africa.”; (3) “Umbilo / 17.X.15”; (4) “Pres. by / Imp. Bur. Ent. / Brit. Mus. / 1924-306.”; (5) “Durb / Mus”; (6)





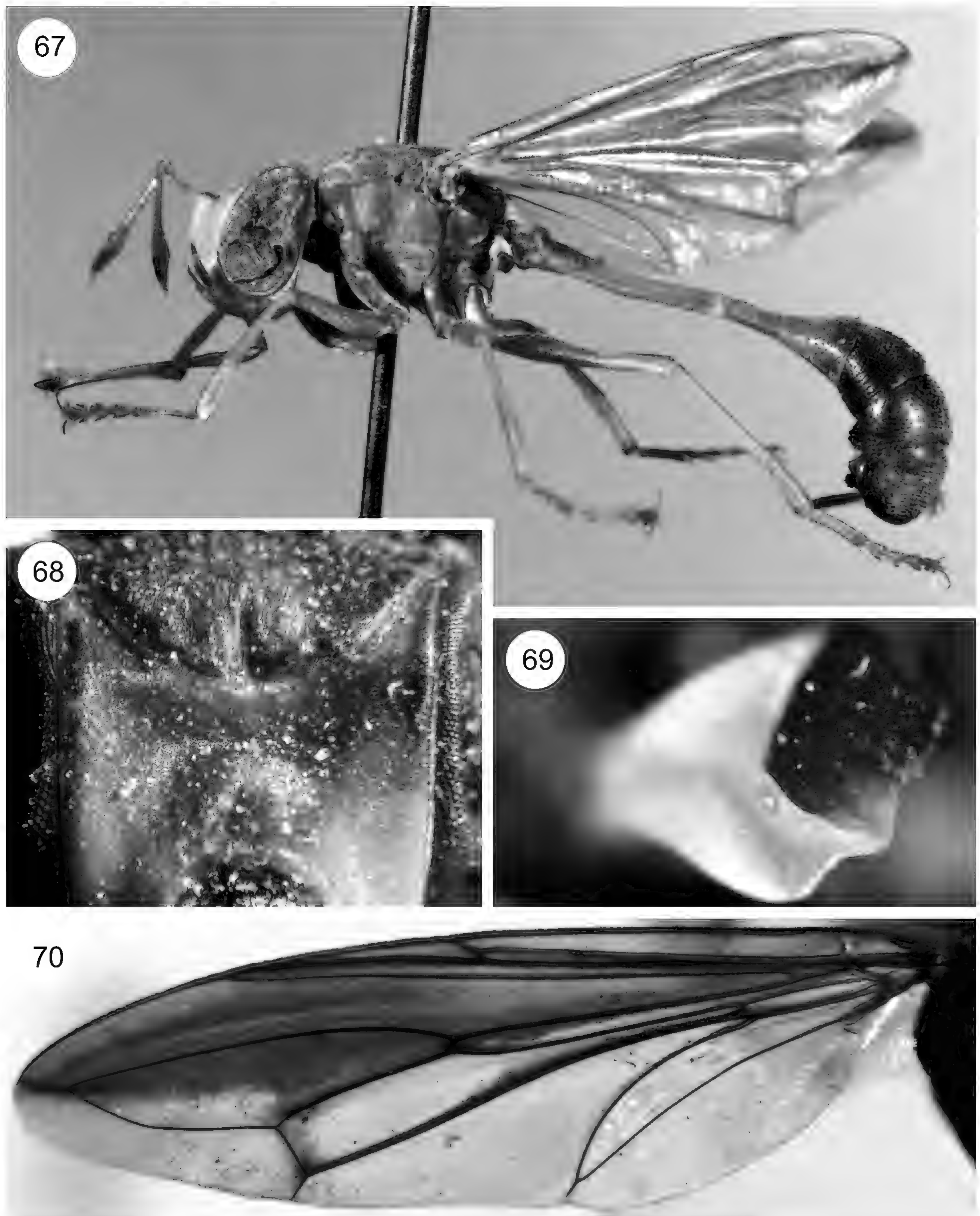
Fig. 66. Head of *Physocephala congoensis* Kröber, 1936, anterolateral view (♂, Bururi).

“*Physocephala / halterata* / Brun Type ♀”; (7) BMNH(E)#/ 249078; coll. NHML

**Additional Material.** BURUNDI: 1♀, 23.iv.1955, Gitega [=Kitega], 1700 m, leg. F. J. François, coll. ISNB; DEMOCRATIC REPUBLIC OF CONGO: 1♀, 6.iii.1948, Katanga Province, Mukana, Lusinga, 1810 m, leg. G. F. de Witte, coll. ISNB; 1♀, 15.iii.1948, ditto; ETHIOPIA: 1♀, 4.xii.2014, Bonga Waldaum, 1628 m [07°11.87'N 036°15.13'E], *Bothriocline schimperi*, leg. H.-J. Flügel, coll. PHJF; KENYA: 1♀, 25.ix.2005, Kericho junction [0°23'S 35°16'E], 1530 m, leg. L. Friedman, coll. TAUI; 1♂, 23.v.1910, Muguga, det. as *P. halterata* by Camras 2000, [collector unknown], coll. NHML [NHMUK010922109]; 1♀, vii.1937, Nairobi, det. as *P. halterata* by Camras 2000, leg. V. G. L. van Someren, coll. NHML [NHMUK010922121]; 1♂, vii.1937, Nairobi, leg. van Someren, coll. NHML [NHMUK010922111]; LESOTHO: 1♂, 30.xii.1950, Mamathes [-29.136617 27.845796], leg. C. Jacot-Guillarmod, coll. AMGS; 1♀, 4.xi.1951, ditto; 2♂♂, 9.xi.1951, ditto; 1♂, 11.xi.1951, ditto; 2♀♀, 3.ii.1952, ditto; 1♂, 15.ii.1952, ditto; 1♀, 11.xi.1952, ditto; 2♂♂, 23.xi.1952, ditto; 1♂, 14.xi.1954, ditto; SOUTH AFRICA: 1♂, 1906, Transvaal, leg. A. J. Chalmley, coll. NHML [NHMUK010922113]; 1♀, 6.–7.i.1993, Cape Province, Cape of Good Hope Nat. Res., leg. F. Koch, coll. ZMHB; 1♂, 12.xi.1952, Cape Province,

Grahamstown, leg. C. Jacot-Guillarmod, coll. AMGS; 1♂, 23.i.1970, Cape Province, Grahamstown, Belmont Valley, on flowering *Foeniculum vulgare* Mill., leg. C. Jacot-Guillarmod, coll. AMGS; 1♂, i.1922, Cape Province, Mossel Bay, det. as *P. halterata* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922114]; 1♀, iv.1933, Cape Province, Mossel Bay, det. as *P. halterata* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922117]; 1♀, 1.–14.xi.1921, Cape Province, Mossel Bay, det. as *P. halterata* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922120]; 1♀, 22.iii.1939, Cape Province, Mossel Bay, det. as *P. halterata* by Camras 1962, leg. R. E. Turner, coll. NHML [NHMUK010922124]; 1♂, 29.i.–5.ii.1924, Eastern Cape Province, Port St. John, Bondoland, det. as *P. halterata* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922115]; 1♀, 6.–25.ii.1924, Eastern Cape Province, Port St. John, Bondoland, det. as *P. halterata* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922119]; 1♀, ii.1927, Free State Province, Harrismith, det. as *P. halterata* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922118]; 1♀, 10.x.2004, Gauteng Province, Benoni [26°08'S 28°23'E], leg. C. Midgley, coll. AMGS; 1♂, ii.1897, Natal Province, Karkloof, [collector unknown], coll. NHML [NHMUK010922110]; 1♀, 25.–31.iii.2001, Northern Province, Lekgalameetse Reserve [24°12'S 30°20'E],





**Figs 67–70.** *Physocephala halterata* Brunetti, 1925 (♂, Mamathes). **67.** Habitus, lateral view; **68.** Frons, dorsal view; **69.** Haltere, lateral view; **70.** Wing, dorsal view.



leg. F. Koch, coll. ZMHB; TANZANIA: 1♂, end of xii.1898 to end of i 1899, Nyasasee, Langenburg [= Tukuyu], det. as *P. congoensis* by Camras 2000, leg. S. Fülleborn, coll. ZMHB; 1♀, 24.xi.1963, Iringa Region, Ulete, det. as *halterata* by Camras 2000, leg. D. J. Greathead, coll. NHML [NHMUK010922122]; UGANDA: 1♂, 13.ii.1966, Lake Nabugabo, leg. D. J. Greathead, coll. NHML [NHMUK010922112]; ZIMBABWE: 1♂, 10.1926, Chirinda Forest, det. as *P. halterata* by Bryant, leg. G. Arnold, coll. NHML [NHMUK010922116]; 1♀, 16.–18.iii.2001, Vumba Mountain, Botanical Garden [19°07'S 32°47'E], leg. F. Koch, coll. ZMHB; UNKNOWN LOCATION: 1♀, 25.v.1901, [characters illegible], det. as *P. halterata* by Kröber 1938, [collector unknown], coll. NHML [NHMUK010922123].

### *Physocephala microvena* species-group

This species-group combines some of the species which were variously placed by Camras (2001) in his *Pseudophysocephala nigratarsis*, *Pseudophysocephala platycephala* and *Physocephala simplex* species-groups. Members of this group cannot be defined by single characters but by a combination of characters as set out in Key 1. A reduced or absent radial-medial crossvein, and therefore either a reduced vena spuria or a vena spuria that lies very close to the radius  $R_{4+5}$ , is typical, however. Almost always there is no hyaline wing membrane between the vena spuria and radius  $R_{4+5}$  and the aristomeres are elongated, with the apical aristomere usually towering over the basal aristomere. The group contains some very difficult species, several of which can readily be confused with members from other species-groups, and more material is necessary in order to understand the full variability of the species. All members of this group are restricted to the Afrotropical Region.

### Key 6 – Identification of the *Physocephala microvena* species-group

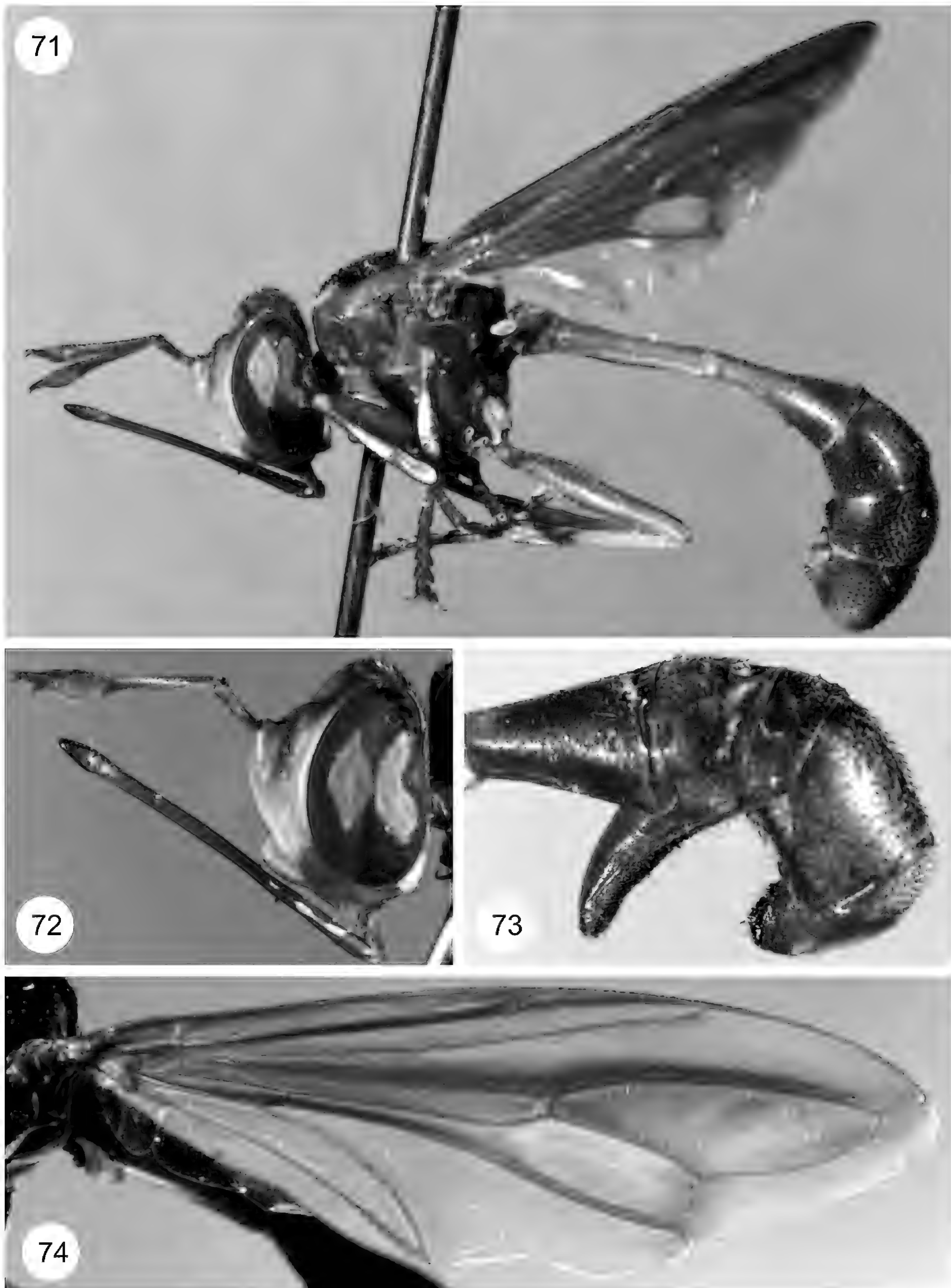
1. Face with deep black stripe extending from antennal base to mouth edge, clearly separated from yellow lateral part of facial groove (e.g. Fig. 92); hind femur with a wide blackish ring in apical half, fore and middle femora with distinct black spots (e.g. Fig. 91); dusting stripe on pleura not evident; vertex almost entirely covered with long setulae and with a roughened surface, although lacking longitudinal grooves; margin of scutum and scutellum light orange to brown (e.g. Fig. 91); cell  $r_{2+3}$  completely brown (e.g. Fig. 93)..... **2**
- Face sometimes black but never with such a distinct and deep black stripe; femora without such black markings; other characters variable but never in the above combination ..... **3**

2. Discal-medial-cubital crossvein not completely surrounded by brown colouration (Fig. 93); radial-medial crossvein usually absent, radius and media fused (Fig. 93); scape and pedicel light orange (Fig. 91); tarsi concolourous with tibiae, orange-brown (Fig. 91); proboscis completely orange to brown, lacking contrasting black labellum (Fig. 91); scutum anteriorly with submedial pair of dull lines caused by microtrichia; ♂ tergites 3–5 densely dusted (anterior view), tergite 2 densely dusted (posterior view) and with a complete dusting band at its hind margin; ♂ epandrium with isolated black tooth submedially on posterior margin ..... ***P. kroeberi* nom. nov.**
- Discal-medial-cubital crossvein completely surrounded by brown colouration; radial-medial crossvein developed, radius and media therefore separated; scape and pedicel mainly black to dark brown; tarsi distinctly darker than tibiae; proboscis black in apical half; scutum anteriorly lacking submedial pair of dull lines caused by microtrichia; ♂ tergite 3 only lightly dusted, tergite 2 lacking dusting band at hind margin; no obvious black tooth submedially on posterior margin of ♂ epandrium..... ***P. discalis* (Camras, 1962)**
3. ♂ narrow base of abdomen (from tergite 1 to end of parallel-sided anterior part of tergite 3, Fig. 75) only about half as long as the broad apical part of the abdomen; ♀ unknown ..... ***P. brevipetiolata* (Camras, 1962)**
- Narrow base of abdomen (as measured above, e.g. Figs 78, 94) more than half as long as the broad apical part of the abdomen ..... **4**
4. ♂ abdominal segments short, hind margin of tergite 3 almost as long as lateral margin (e.g. Fig. 78); ♂ tergites 4–5 densely dusted (anterior view); tergite 3 sometimes densely dusted (usually in posterior view) and has a complete dusting band at its hind margin (e.g. Fig. 78); ♀ abdomen obviously narrows apically in dorsal view (e.g. Fig. 76); ♀ theca small, not projecting far ventrally (e.g. Fig. 77); ♂ epandrium with isolated black tooth submedially on posterior margin (e.g. Fig. 82); epandrium in dorsal view as e.g. Fig. 82; radial-medial crossvein sometimes short but is always distinct; costa and subcosta usually orange-brown; cell  $r_{2+3}$  completely brown (e.g. Fig. 83); proboscis orange to brown, with contrasting black labellum; legs including tarsi orange-brown; face with more or less large brown to black mark; gena typically light brown, darker than yellow parafacia; frons with a more or less obvious brown mark reaching from vertex to base of antennae; scutum with three fused or separated blackish spots, margin of scutum and scutellum always light orange (e.g. Fig. 81); scutum anteriorly may have submedial



- dull lines caused by microtrichia (e.g. Fig. 81); where such lines occur, the distance between them is almost as wide as the lines themselves ..... 5
- ♂ abdominal segments usually longer, hind margin of tergite 3 shorter than lateral margin (e.g. Figs 94, 106); ♂ tergites 3–4 hardly to distinctly dusted, tergite 2 at most indistinctly dusted and may lack a complete dusting band at its hind margin (e.g. Figs 94, 106); ♀ abdomen not obviously narrowing apically in dorsal view (e.g. Fig. 95); ♀ theca always larger, and usually projecting further ventrally (e.g. Fig. 96); ♂ epandrium lacking black tooth, or with tooth situated on an elongated blackish keel on posterior margin (e.g. Fig. 101); epandrium in dorsal view sometimes different; radial-medial crossvein sometimes completely absent (e.g. Fig. 101); costa and subcosta sometimes dark brown like other veins; cell  $r_{2+3}$  may be hyaline in apical third; proboscis sometimes completely brown to black, lacking a distinctly darker labellum; legs and tarsi sometimes completely black, or with obvious black markings; face sometimes completely yellow to orange-brown; gena sometimes yellow or orange-brown like parafacia; frons may have no dark marking, or is sometimes almost completely black to brown; margins of scutum and scutellum sometimes black or dark brown; scutum anteriorly with or without submedial dull lines caused by microtrichia. Where such lines occur these are only separated very narrowly (e.g. Fig. 99)..... 6
5. Three separate blackish spots on scutum (Figs 103, 105); ♀ theca about as broad as width of tergite 7 (Fig. 102), posterior surface with strong black setulae less dense so that the underlying surface is visible, ventral margin and posterior surface with long setae irregularly arranged; ♀ postabdomen elongated in side view, apical tergites tapered in dorsal view (Figs 102–104) ..... ***P. platycephala* (Loew, 1853)**
- Black spots on scutum more or less fused (Fig. 81); ♀ theca narrower than width of tergite 7 (Fig. 77), posterior surface with strong black setulae densely packed so as to obscure underlying surface, ventrolateral margin with long setae regularly arranged in a line, about the same distance from each other; ♀ postabdomen not obviously elongated in side view, apical tergites sharply narrowed in dorsal view (Figs 76–77) ..... ***P. constricta* Kröber, 1915**
6. Vertex usually with distinct longitudinal grooves and always lacking distinct dense punctiform indentations (cf Fig. 87); cell  $r_{2+3}$  completely brown (e.g. Fig. 107); radial-medial crossvein sometimes completely absent, and radius and media fused (e.g. Fig. 107); frons with a delimited black to light brown marking from vertex to base of antennae, becoming narrower anteriorly; ♀ theca short and broad, field of black setae on sternite 4 about three times as broad as long (e.g. Figs 96, 97); ♀ tergite 6 obviously shorter than tergite 4 in side view (e.g. Fig. 96)..... 7
- Vertex usually lacking longitudinal grooves but with distinct dense punctiform indentations (e.g. Fig. 87); cell  $r_{2+3}$  sometimes hyaline apically (e.g. Fig. 89); radial-medial crossvein usually present (although may be very short) and therefore media and radius not touching (e.g. Fig. 89); frons sometimes almost completely darkened; ♀ theca longer and narrower, field of black setae of sternite 4 at most about two times as broad as long; ♀ tergite 6 obviously longer than tergite 4 in side view (e.g. Figs 73, 88)..... 8
7. Dusting stripe on pleura more or less distinct, reaching from middle coxa to notopleuron; margin of scutum and scutellum orange and distinctly delimited from blackish central scutum; scutum anteriorly with submedial dull lines caused by microtrichia (Fig. 99); abdomen partly orange-brown to light brown, grading into dark brown or blackish areas (Figs 94, 95); tergites 3 and 4 with distinct dusted hind margins or strongly dusted all over, tergite 5 and protandrium (♂) or tergite 6 (♀) completely dusted (all in dorsal view, Fig. 94, 95); ♂ epandrium with distinct black tooth standing on an elongated blackish keel on posterior margin (Fig. 101) ..... ***P. microvena* Brunetti, 1925**
- Dusting stripe on pleura absent or only poorly developed; margin of scutum and scutellum completely black or dark brown, and not obviously delimited from black centre (Fig. 106); scutum anteriorly lacking submedial dull lines caused by microtrichia; abdomen uniformly blackish to dark brown (Fig. 106); tergite 3 may have an indistinctly dusted hind margin, abdomen otherwise shining to only very lightly dusted; ♂ epandrium not examined ..... ***P. pseudomicrovena* Kröber, 1939**
8. Smaller species, wing length less than 7 mm..... ***P. digitata* (Speiser, 1909)**
- Larger species, wing length about 8 mm ..... 9
9. Face yellow, without dark spot (Fig. 72); gena sometimes completely brown, in all specimens examined there is at least some brownish colouration; pleura lightly dusted all over but without obvious dense dusting; scutum anteriorly without submedial dull lines caused by microtrichia; tergite 3 lacking large silver dusting spots in posterior lateral corners; discal-medial-cubital crossvein more or less brown infuscated (Figs 71, 74); ♀ theca exceptionally long (Fig. 73)..... ***P. abyssinica* Kröber, 1915**
- Face with dark spot; gena sometimes completely yellow, at most with some brown colouration but





**Figs 71–74.** *Physocephala abyssinica* Kröber, 1915. **71.** ♀ habitus, lateral view (♂, n Vumba); **72.** ♀ head, lateral view (♂, n Vumba); **73.** ♀ theca, lateral view (♀, Albertville); **74.** Wing, dorsal view (♂, n Vumba).



never completely brown; katepisternum strongly silver dusted in posterolateral corner; scutum anteriorly with submedial dull lines caused by microtrichia; tergite 3 with large silver dusted spots in posterior lateral corners; discal-medial-cubital crossvein not brown infuscated in the specimens examined; ♀ theca not exceptionally long.....

.....*P. maculifacies* Camras, 2001

***P. abyssinica* Kröber, 1915**

(Figs 71–74)

*Physocephala abyssinica* Kröber 1915

= *Physocephala fumivena* Camras 2001 (**syn. nov.**)

= *Physocephala longithea* Camras 2001 (**syn. nov.**)

= *Physocephala atronata* Camras, 2001 (**syn. nov.**)

**Primary type material examined.** ♀ holotype of *Physocephala longithea* Camras, 2001: (1) “Angola (A37) / 5 mls. NE. Negola / 25.iii.1972”; (2) “Southern / African Exp. / B. M. 1972–1”; (3) “Holotype ♀ / *Physocephala longithea* / Camras”; coll. NHML.

♂ holotype of *Physocephala atronata* Camras, 2001: (1) “W. Uganda / Kibale Forest / 12.xii.1971 – 9.i.1972 / R. L. Mason”; (2) “Holotype ♂ / *Pseudophysocephala atronata* / Camras”; coll. NHML.

**Additional material.** DEMOCRATIC REPUBLIC OF CONGO: 2♀♀, 1.–20.i.1919, Albertville [= Kalemi], 780 m, det. as *P. “? abyssinica”* by Brunetti 1925, leg. R. Mayné, coll. MRAC; 1♂, x.1932, Lulua, Kapan-ga, det. as *P. “? abyssinica* Krb” by Kröber 1935, leg. F. G. Overlaet, coll. MRAC; MALAWI: 1♂, 4.x.1919, Nyasaland, Cholo. [= Thyolo District], det. as *P. “? abys-sinica”* by Brunetti 1924, leg. R. C. Wood, coll. NHML [NHMUK010922100]; UGANDA: 1♀, 21.i.1913, West Mengo District, Entebbe, det. as *P. “? abyssini-ca”* by Brunetti 1924, leg. C. C. Gowdey, coll. NHML [NHMUK010922101]; ZIMBABWE: 1♂, 2.i.1966, n Vumba [= Bvumba] [-19.093432 32.740631], paratype of *P. fumivena*, leg. D. Cookson, coll. FMNH.

*Physocephala abyssinica* is easily recognised in the female by the very long theca (Fig. 73) but is difficult to identify in the male. Camras (2001) failed to recognize that females of his newly described *P. longithea* were in fact conspecific with males previously identified as *P. abys-sinica*. Instead he described the males again as *P. fumi-vena* – a species in which only males are known. The only character given by Camras (2001) to distinguish *P. fumivena* and *P. longithea* is the wing colouration, with a dark infuscated discal-medial-cubital crossvein being present in *P. fumivena*. It is clear that this character is very variable, however, in which case there is no other published character left to distinguish these two species either from each other or from *P. abysinica*, and we cannot find any such characters in the material we

have to hand, which includes the holotype of *P. longithe-ca* and a paratype of *P. fumivena*. Therefore, *Physoceph-ala longithea* Camras 2001 and *Physocephala fumi-vena* Camras, 2001 are both placed as junior synonyms of *Physocephala abyssinica* Kröber, 1915 (**syns. nov.**).

In addition, Camras (2001) also characterised *P. atro-nata* with the character “Haltere with black on club”. In fact there is only slight darkening on the haltere of the holotype, which is quite different from the velvety black haltere of species in the *P. halterata* species-group. The holotype of *P. atronata* otherwise fits very well with specimens of *P. abyssinica* and therefore *Physocephala atronata* Camras, 2001 is also herewith placed as a ju-nior synonym to *Physocephala abyssinica* Kröber, 1915 (**syn. nov.**).

***P. brevipetiola* (Camras, 1962)**

(Fig. 75)

*Pseudophysocephala brevipetiola* Camras, 1962

**Primary type material examined.** ♂ holotype of *Pseu-dophysocephala brevipetiola* Camras, 1962: (1) “♂ / Ho-lotypus”; (2) “Musé du Congo / Eala / III-1932 / H. J. Bredo”; (3) “Holotype ♂ / *Pseudophysocephala brev-i-petiola* / Camras”; (4) “RMCA ENT / 000012177”; coll. MRAC.

**Additional Material.** GABON: 1♂, viii.1892, Libre-ville, determined as a *Physocephala* nov. spec. by Kröber 1921, [collector unknown], coll. MLUH.

*Physocephala brevipetiola* is a rarely recorded species. Only the two males mentioned above are known to date. These are obviously well characterised by the unique ab-domen shape, having a very narrow base of the abdomen (“petiole” *sensu* Camras (1962), cf Fig. 75) which is ob-viously much shorter than remaining bulbous abdomen (“abdominal club” *sensu* Camras 1962).

***P. constricta* Kröber, 1915**

*Physocephala constricta* Kröber 1915

= *Physocephala ruficoxa* Kröber, 1933

(Figs 76–83)

**Primary type material examined.** ♀ lectotype of *Phys-ocephala constricta* Kröber 1915 designated by Camras (2001): (1) “3053”; (2) “Type”; (3) “*Physocephala* ♀ / *constricta* Krb. / O. Kröber det. 1914”; coll. ZMHB.

♂ holotype of *Physocephala ruficoxa* Kröber 1933: (1) “Holo - / type”; (2) “Lady Grey / 3 Feb. 1925. / R. I. Nel”; (3) “Pres. By / Imp. Inst. Ent. / Brit. Mus. / 1932-143”; (4) “*Physocephala ruficoxa* Kröb / det. Kröber 1930”; (5) “Type”; (6) “*Pseudophysocephala constricta* Kröber / compared to type / det. Camras, 2000”; coll. NHML.



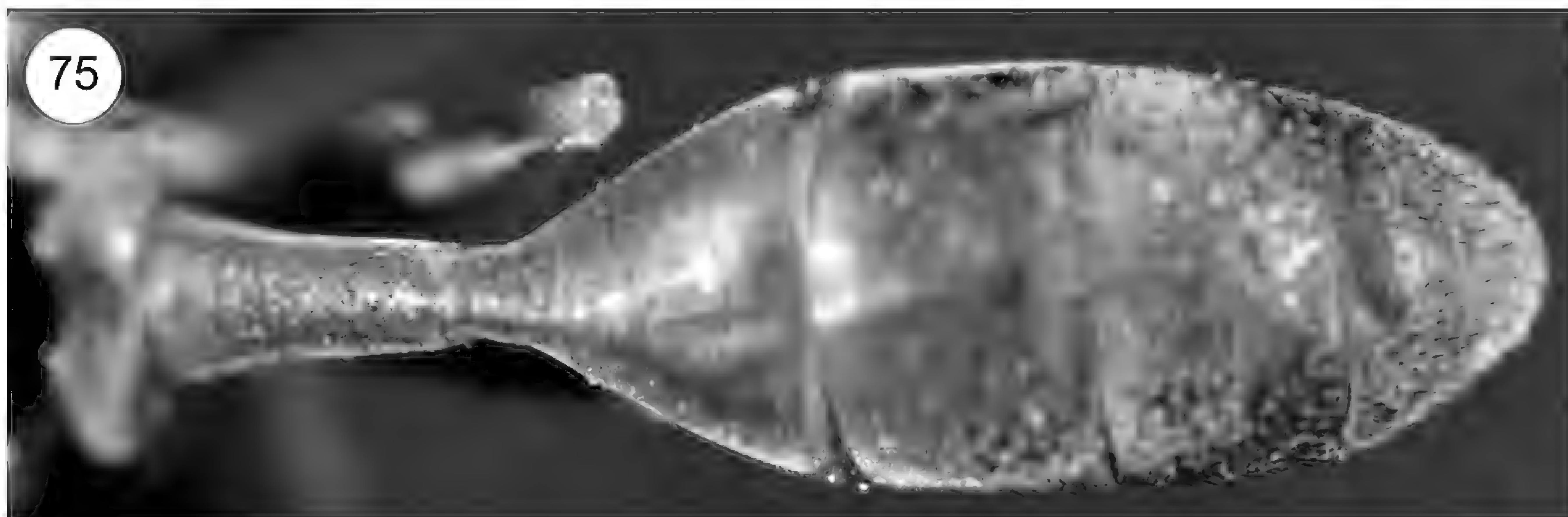


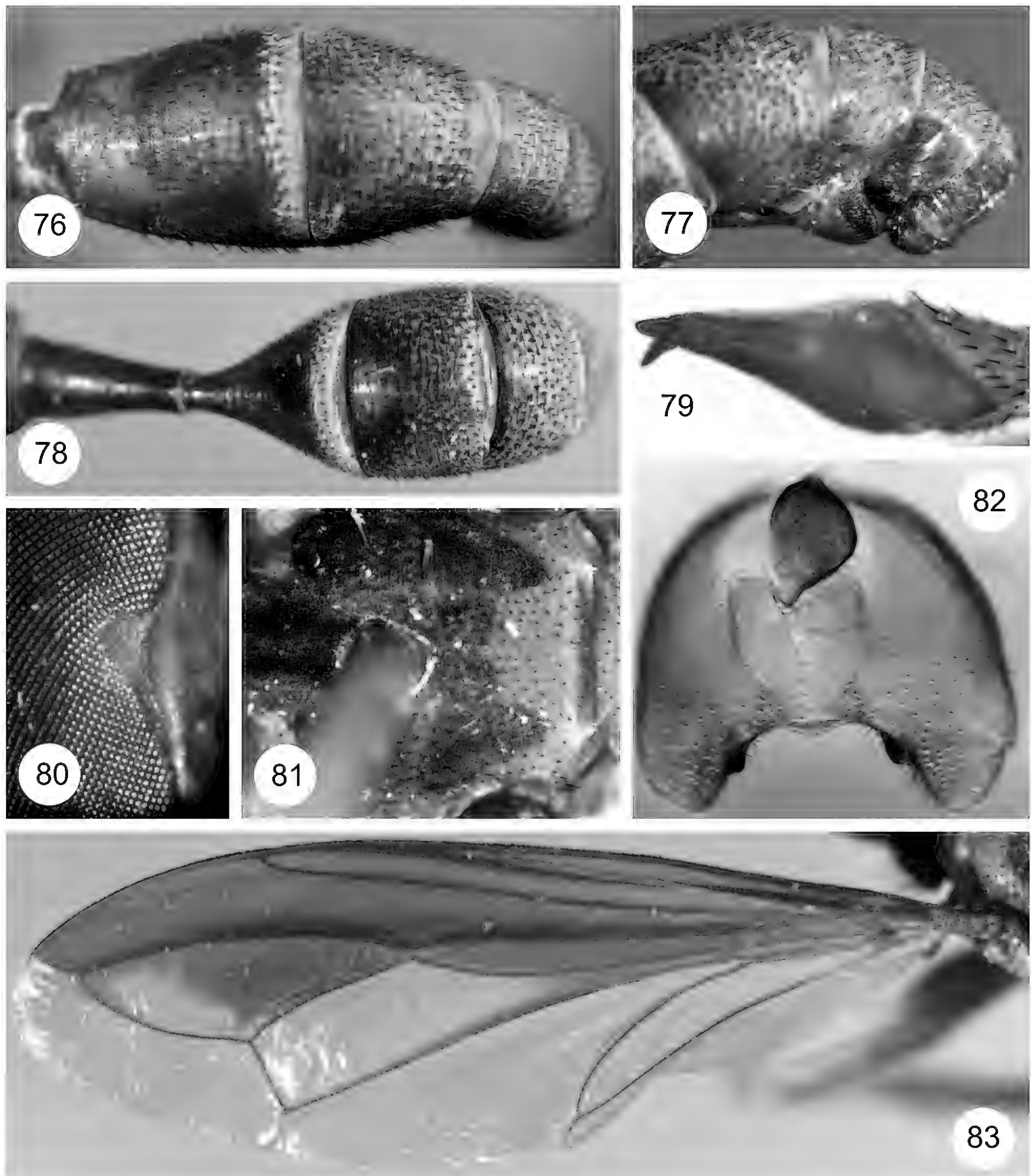
Fig. 75. Abdomen of *Physocephala brevipetiolata* (Camras, 1962), dorsal view (♂, Libreville).

**Additional material.** LESOTHO: 1♂, 13.xi.1949, Mamathes [-29.136617 27.845796], leg. C. Jacot-Guillarmod, coll. AMGS; 1♂, 7.xi.1951, Mamathes [-29.136617 27.845796], leg. A. Jacot-Guillarmod, coll. AMGS; 2♂♂, 3.ii.1952, Mamathes [-29.136617 27.845796], leg. C. Jacot-Guillarmod, coll. AMGS; 1♂, 11.ii.1952, ditto; 1♂, 23.xi.1952, ditto; 1♂, 15.iii.1951, Quthing, det. as *P. spec.*, *interrupta* group by Smith 1966, leg. Brink, Rudebeck, coll. MZLU; 1♂, 12.iii.1951, Sebalabala, leg. C. Jacot-Guillarmod, coll. AMGS; 1♂, 8.–14.i.1963, Maseru district, Bushmans Pass, Maloti Mountains, 2125–2250 m, det. as *P. lineifrons* by Camras 1963, leg. B. R. Stuckenberg, P. J. Stuckenberg, coll. FMNH; SOUTH AFRICA: 1♂, “3053” [? Cape], paralectotype of *P. constricta*, leg., coll. ZMHB; 1♀, iii.1959, Cathedral Peak, Forestry reserve, Natal Drakensberg Little Berg summits, themeda Grassland, 5500–6000 ft, det. as *P. constricta* by Camras 1962, leg. B. R. Stuckenberg, P. J. Stuckenberg, coll. PJHS; 1♂, 10.–12.xi.2009, Cape Province, Harrismith Scotland farm [27°58'59.5"S 29°37'09.8"E], Malaise trap, dense *Leucosidea* dominated scrub, leg. A. H. Kirk-Spriggs, coll. BMSA; 1♂, 1.–10.ii.1933, Eastern Cape Province, Katberg, det. as *P. constricta* by Kröber 1938, det. as *P. constricta* by Camras 2000, leg. R. E. Turner, coll. NHML [NHMUK010922174]; 1♂, 1.–10.ii.1933, Eastern Cape Province, Katberg, det. as *P. constricta* by Kröber 1938, det. as *P. constricta* by Camras 2000, leg. R. E. Turner, coll. NHML [NHMUK010922175]; 1♂, 1.–10.ii.1933, Eastern Cape Province, Katberg, det. as *P. constricta* by Kröber 1938, det. as *P. constricta* by Camras 2000, leg. R. E. Turner, coll. NHML [NHMUK010922177]; 1♂, 1.–10.ii.1933, Eastern Cape Province, Katberg, det. as *P. constricta* by Kröber 1938, det. as *P. constricta* by Camras 2000, leg. R. E. Turner, coll. NHML [NHMUK010922178]; 1♀, 19.–26.ii.1933, Eastern Cape Province, Katberg, det. as *P. ruficoxa* by Kröber 1938; det. as *P. constricta* by Camras 2000, leg. R. E. Turner,

coll. NHML [NHMUK010922173]; 1♂, 6.i.1925, Eastern Cape Province, Lady Grey, paratype of *P. ruficoxa*, leg. R. I. Nel, coll. NHML [NHMUK010922180]; 1♂, 26.i.1960, Eastern Cape Province, Molteno, leg. M. D. Anderson, coll. AMGS; 1♂, 4.–5.ii.1992, Eastern Cape Province, Rhode, village area [30°48'S 27°58'E], 1820 m, det. as *P. constricta* by Camras 2000, leg. Natal Museum Expedition, coll. FMNH; 1♂, 22.i.1965, Free State Province, Senekal, leg. D. J. Brother, coll. AMGS; 1♂ 1♀, 12.ii.2016, KwaZulu-Natal Province, Garden Castle N. R., Sleeping Bea [29°44'56'S 29°10'35"E], 2190 m, leg. RSA-team Ståhls, coll. PASS; 1♂, 4.xii.2012, KwaZulu-Natal Province, Royal Natal National Park, day visitor Ca [28°41'25.4"S 28°56'53.9"E], 1410 m, Paratype, leg. A. Ssymank, coll. PASS; 1♀, 20.–21.xi.2003, Mpumalanga Province, 20 km sw Lydenbrug, leg. J. Halada, coll. CULSP; 1♂, iii.1933, Natal Province, Natal, Nationalpark, det. as *P. constricta* by Camras 2000, leg. J. Ogilvie, coll. NHML [NHMUK010922179]; 1♂, 13.iv.1963, Northwest Reg., Retiefs Kloof, Rustenburg, leg. H. N. Empey, coll. PMHA; UNKNOWN LOCATION: 1♂, “3054”, det. as *P. platycephala* by Kröber 1914, wrongly labelled as allotype of *P. platycephala*, leg., coll. ZMHB; 2♀♀, “AcP 5470”, leg., coll. NHML; 1♀, no date, “AcP 5470”, [collector unknown], coll. NHML; 1♂, 13.xi.1954, [characters illegible], det. as *P. constricta* by Camras 2000, leg. K. G. V. Smith, coll. NHML [NHMUK010922176].

Females of *P. constricta* are easily identified by the unique shape of the abdomen and theca as described in Key 6 (Figs 76, 77). Males are extremely difficult to diagnose, however, and can be confused with members of the *abdominalis*, *microvena*, *caenoneura* and *antiqua* species-groups. Males of *P. constricta* should be compared very carefully, bearing in mind that not all specimens can be reliably assigned to species.





**Figs 76–83.** *Physocephala constricta* Kröber, 1915. 76. ♀ abdomen, dorsal view (♀, Cathedral peak); 77. Tip of ♀ abdomen, lateral view (♀, Cathedral peak); 78. ♂ abdomen, dorsal view (♂, Harrismith Scotland farm); 79. Arista, lateral view (♂, Harrismith Scotland farm); 80. Indentation on posterior margin of eye, lateral view (♀, Cathedral peak); 81. Scutum, dorsal view (♂, Harrismith Scotland farm); 82. Epandrium, dorsal view (♂, Mamathes); 83. Wing, ventral view (♀, Cathedral peak).

***P. digitata* (Speiser, 1909)**

(Figs 84–90)

*Conops (Physocephala) digitatus* Speiser 1909

= *Physocephala simplex* Kröber, 1915 (**syn. nov.**)

= *Physocephala ugandae* Kröber, 1915 (**syn. nov.**)

= *Physocephala nigricoxa* Brunetti, 1925



= *Physocephala bequaertorum* Camras, 1962 (**syn. nov.**)  
 = *Physocephala lineifrons* Camras, 1962 (**syn. nov.**)  
 = *Physocephala ethiopica* Camras, 1962 (**syn. nov.**)

**Primary type material examined.** ♂ holotype of *Pseudophysocephala ugandae* Kröber 1939: (1) “*Psilocephala* [sic] / *ugandae*, Krb. / examined & det. / O. Kröber, 1938.”; (2) “*Psilocephala* [sic] / *ugandae* / Krb.”; (3) “Uganda, / Kampala, / 6.IX.1918. / C C. Gowdey.”; (4) “Kampala, / Uganda / 6.IX.1918 / No. 6545”; (5) “Pres. by / Imp. Bur. Ent. / Brit. Mus. / 1921-153”; (6) “Type”; coll. NHML.

♂ holotype of *Physocephala nigricoxa* Brunetti, 1925: (1) “Syn- type”; (2) “Kampala, / Uganda / 4.IX.1918 / C. C. / No. 5392 Gowdey”; (3) “Pres. by / Imp. Bur. Ent. / Brit. Mus. / 1924-306.”; (4) “*Physo.* / *nigrocoxae* [sic] / Brun Type ♂ / Det. E. Brunetti 1924”; coll. NHML. There is a second damaged specimen lacking both head and abdomen that is designated as “Syntype”. This cannot be identified but in any event, in the original description the specimen listed above as the holotype is explicitly identified as the “Type”.

♀ holotype of *Physocephala ethiopica* Camras, 1962, pinned together with ♂ paratype: (1) “Holo- / type”; (2) “Allo- / type”; (3) “Ethiopia: / Dilla, / (Sidamo). / iv.1948.”; (5) “Holotype ♀ / *Physocephala* / *ethiopica* / Camras”; (6) “Allotype ♂”; (7) “K. M. Guichard / B. M. 1948-200.”; (8) “[characters illegible]”; (9) “BMNH(E)# / 249079 / BMNH(E)# / 249080”; coll. NHML.

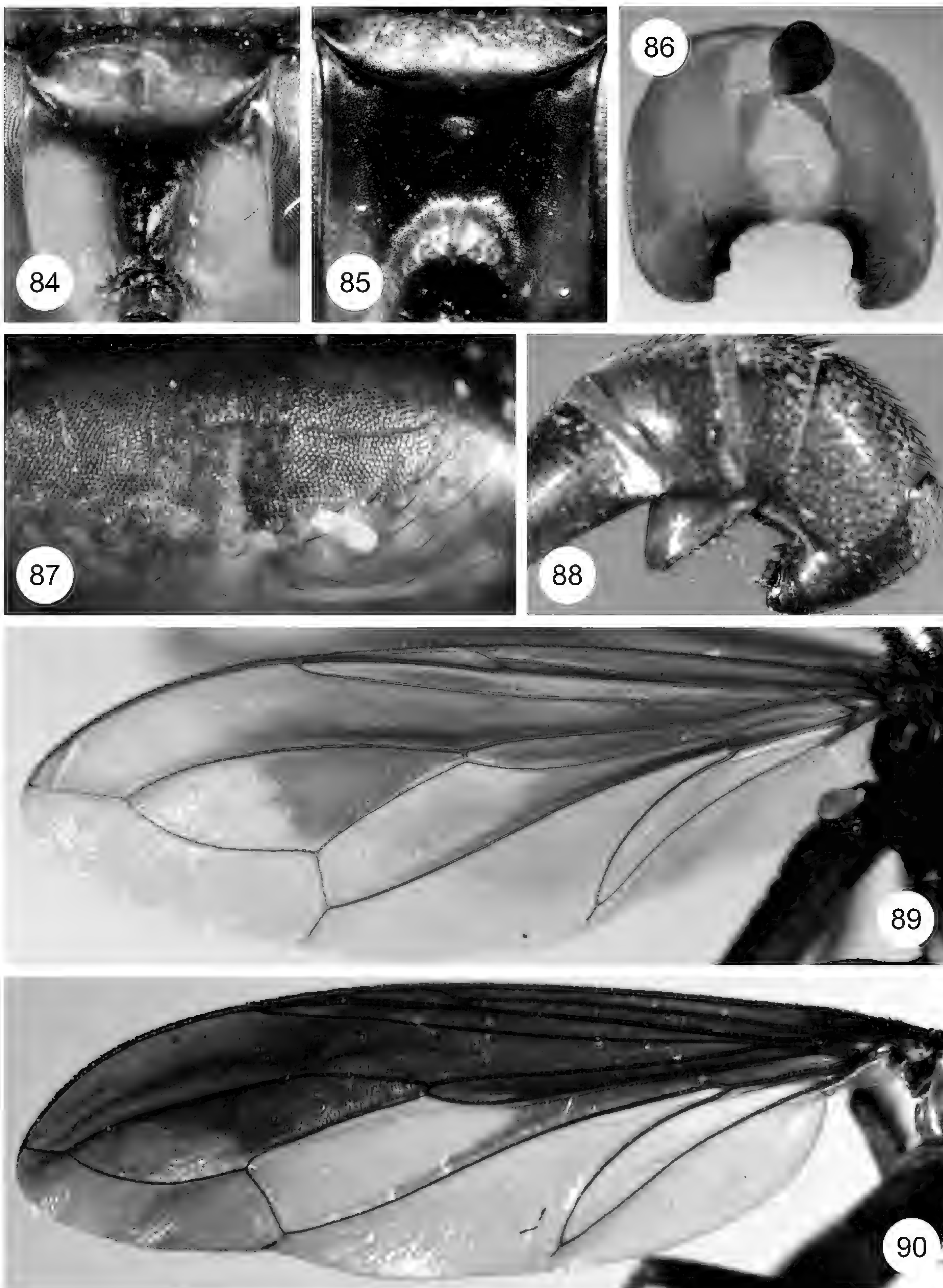
**Additional material.** BURUNDI: 1♀, V.1956, Mugeru, leg. F. J. François, coll. ISNB; CAMEROON: 1♀, 30.vii.1920, Lolodorf, det. as *P. simplex* by Camras 1962, leg. A. I. Good, coll. FMNH; 1♂, 8.–10.viii.2013, Far-North Reg., Mayo-Tsanga, Mogode-Cha [10°34.111'N 13°36.422'E], 1001 m, Malaise trap, degraded savanna forest, leg. A. H. Kirk-Spriggs, coll. BMSA; DEMOCRATIC REPUBLIC OF CONGO: 2♂♂, 15.ix.1933, Bambesa, det. as *P. ugandae* by Kröber 1935, leg. J. V. Leroy, coll. MRAC; 1♀, 16.iii.1948, Basoko, Yamabuki, Div. 153, det. as *P. simplex* by Camras 1962, leg. P. L. G. Benoit, coll. MRAC; 1♂, 27.iv.1914, Beni [0°30'N 29°30'E], det. as *P. bequaertorum* by Camras 2000, leg. J. Bequaert, coll. FMNH; 1♀, 23.i.1927, Elisabethville [Lubumbashi] [-11.664232 27.482626], det. as *P. ugandae* by Kröber 1935, leg. M. Bequaert, coll. MRAC; 1♂, 4.iii.1936, Kamogobe, Sud Masisi, det. as *P. nigricoxa* by Camras 1962, leg. L. Lippens, coll. MRAC; 1♂, 18.vii.1935, Kivu, Nyongera, près Rutshuru, 1218 m, leg. G. F. de Witte, coll. ISNB; 1♂, 10.vii.1935, Kivu, Ritshuru, riv. Musugereza, 1100 m, leg. G. F. de Witte, coll. ISNB; 1♂, 10.vii.1935, Kivu, Ritshuru, riv. Musugereza, 1100 m, det. as *P. nigrocoxalis* by Vanschuytbroeck 1950, leg. G. F. de Witte, coll. MRAC; 1♀, 15.x.1957, Massif Ruwenzori, Bomboka près., Kyandolire, 1650 m, leg. P. Vanschuytbroeck & J. Kekenbosch, coll. MRAC;

1♀, 18.xii.1957, Massif Ruwenzori, riv. Lume, moyenne, 1800 m, leg. P. Vanschuytbroeck, coll. MRAC; 1♀, xi.1937, Rutshuru, det. as *P. digitata* by Camras 2000, leg. J. Ghesquière, coll. FMNH; 1♀, no date, Ville Malela, Chief Casende [5,40S 23,45E], det. as *P. simplex* by Camras, leg. J. Bequaert, coll. FMNH; RWANDA: 1♂, 6.ii.1935, Ruhengeri, riv. Mugara-Kigombe, 1800–1825 m, det. as *P. nigrocoxalis* by Vanschuytbroeck 1950, leg. G. F. de Witte, coll. MRAC; TOGO: 1♂, viii.2015, Kloto, forest area [6°57'31.66"N 0°34'29.75"E], leg. G. Goergen, coll. IITA; 1♀, ii.2002, ditto; 1♀, iii.2017, ditto; 1♂, viii.2008, ditto; 1♂, vi.2016, ditto; UGANDA: 1♂, 22.iv.1966, 20 miles e Mubende, det. as *P. nigricoxa* by Camras 2000; det. as *P. digitata* by Camras 2001, at Chickweed flowers, leg. D. J. Greathead, coll. NHML [NHMUK010922194]; 1♂, 14.v.1958, Bugisu Bugusege, det. as *P. nigricoxa* by Camras 2000; det. as *P. digitata* by Camras 2001, at Chickweed flowers, leg. J. Bowden, coll. NHML [NHMUK010922195]; 1♂, 1.–5.xii.1911, Bugoma Forest, Unyoro, 3700 ft, det. as *P. nigricoxa* by Camras 2000; det. as *P. digitata* by Camras 2001, at Chickweed flowers, leg. S. A. Neave, coll. NHML [NHMUK010922192]; 1♂, 21.iv.1927, Dwoli, det. as *P. nigricoxa* by Camras 2000; det. as *P. digitata* by Camras 2001, leg. H. Hargreaves, coll. NHML [NHMUK010922193]; 1♂, 15.–17.iii.1912, Uganda West, Kibale Region, surrounding Bigodi [N0029209 E3020022], 1400 m, leg. Oehlke, coll. PASS; 1♂, 15.–17.iii.2012, ditto; UGANDA / KENYA: 1♂, v., Elgon, 1700 m, leg. Lindblom, coll. NHRS; ZAMBIA: 7♂♂ 1♀, 12.–15.i.2003, 45 km se Kitwe, leg. J. Halada, coll. CULSP.

*Physocephala digitata* is a species which shows great variation in colouration of the face (with or without dark marking); frons (more or less uniformly yellow to light brown, the latter especially in old specimens, and with distinct black midline or almost completely black); coxae (completely light brown to almost black); scutum (completely black to orange-brown with black centre only); and wing (e.g. cell  $r_{2+3}$  completely brown or hyaline apically, subcosta light orange to dark brown). In all of these variations we find different intermediates and no one of these characters, or combination of characters, can be used to consistently segregate species. Camras (2001) did not mention any character in his key for the *simplex* species-group which is not variable in *P. digitata*. Out of the eleven species he included in his *simplex* species-group key, only three species can be recognised consistently (see Key 6, couplets 8–9) and these three are still difficult to identify convincingly.

The original description of *P. simplex* falls within the variation of *P. digitata* as do the specimens reported by Camras (2001) as *P. simplex*. The holotype of *P. simplex* is stored in the Museo Civico di Storia Naturale “Giacomo Doria” (Stuke 2017) and was not available for exam-





**Figs 84–90.** *Physocephala digitata* (Speiser, 1909). **84.** Frons, light form, dorsal view (♀, Mugera); **85.** Frons, dark form, dorsal view (♀, Kloto); **86.** Epandrium, dorsal view (♂, sw Kitwe); **87.** Vertex, dorsal view (♀, Mugera); **88.** Theca, lateral view (♀, Mugera); **89.** Wing, light form, dorsal view (♀, Mugera); **90.** Wing, dark form, dorsal view (♀, Kloto).



ination. *Physocephala simplex* Kröber, 1915 is, however, placed as a junior synonym of *Physocephala* [*Conops*] *digitata* (Speiser, 1909) (**syn. nov.**).

Most specimens of *P. ugandae* are easily recognised by the wing pattern (Fig. 89) with cell  $r_{2+3}$  hyaline apically, and the frons yellow with a distinct black T-marking (Fig. 84). There are, however, less commonly encountered forms typified by a completely dark cell  $r_{2+3}$  and/or either a completely dark or completely pale frons, together with intermediates. Since this variation does not allow *P. ugandae* to be distinguished from *P. digitata* with any consistency, *Physocephala ugandae* Kröber, 1915 is herewith placed as a junior synonym of *Physocephala* [*Conops*] *digitata* (Speiser, 1909) (**syn. nov.**).

The original description and all of the key characters used by Camras (1962b) to identify *P. bequaertorum* fall within the variation of *P. digitata*. One available headless specimen in FMNH identified by Camras as *P. bequaertorum* also fits to *P. digitata*. *Physocephala bequaertorum* Camras, 1962 is therefore placed as a junior synonym of *Physocephala* [*Conops*] *digitata* (Speiser, 1909) (**syn. nov.**).

The type material of *P. ethiopica* falls within the variation of *P. digitata*. *Physocephala ethiopica* Camras, 1962 is therefore placed as a junior synonym of *Physocephala* [*Conops*] *digitata* (Speiser, 1909) (**syn. nov.**).

The original description of *P. lineifrons* compares it with *P. bequaertorum*, stating that the two differ only in the colouration of the gena and frons. The holotype is deposited in the Natal Museum (KwaZulu-Natal, Pietermaritzburg) and was not available for examination, but the original description of *P. lineifrons* falls within the variation of *P. digitata* and therefore *Physocephala lineifrons* Camras, 1962 is also placed as a junior synonym of *Physocephala* [*Conops*] *digitata* (Speiser, 1909) (**syn. nov.**).

#### ***P. discalis* (Camras, 1962)**

*Pseudophysocephala discalis* Camras 1962

**Material.** UGANDA: 1♂, vii.1945, Bwamba Valley, det. as *P. discalis* by Camras 2000, leg. van Someren, coll. NHML [NHMUK010922150].

The interpretation of this species is based only upon the above specimen in the NHML which was identified by Camras as *P. discalis* following his comparison with the holotype of that species at the USNM.

#### ***P. kroeberi* nom. nov.**

(Figs 91–93)

= *annulipes* (Kröber 1939), junior secondary homonym of *Conops annulipes* Wiedemann in Meigen 1824

**Primary type material examined.** ♂ holotype of *Pseudophysocephala annulipes* Kröber 1939: (1) “Holo- /

type”; (2) “Kinangop / below bamboo / forest 8500 ft”; (3) “Kenya: / Aberdare Range / x.1934. / B. M. E. Afr. Exp. / B. M. 1935-203”; (4) “*Pseudophysocephala / annulipes*. Krb / examined & det. / O. Kröber 1938”; (5) “*Pseudophysoce / phala annuli- / pes* Krb”; (6) [blank red label]; coll. NHML.

**Additional material.** KENYA: 1♂, 22.ix.1990, Mount Kenya, ≈ 10.000 ft, sweep netting, leg. R. Copeland, coll. IITA; 1♀, i.–ii.1946, N. W. Mau Forest, 8000–10000ft, det. as *P. annulipes* by Camras 1962, leg. H. P. Thommas, coll. NHML [NHMUK010922136].

*Physocephala kroeberi* **nom. nov.** is a new name for *Pseudophysocephala annulipes* Kröber 1939 – Kröber (1939): 389; type-locality: “Kenya, Aberdare Range”; HT ♂ [BMNH] – which is a junior secondary homonym of *Conops annulipes* Wiedemann in Meigen 1824: 135; type-locality: “Wahrscheinlich aus Oesterreich”; HT ♂ [depository unknown, Evenhuis 1997] – available, invalid: junior synonym of *Physocephala pusilla* (Meigen, 1804).

*Physocephala kroeberi* is easily recognised by the distinctive black facial marking (Fig. 92), obvious markings on the femora (Fig. 91), and wing pattern with the discal-medial-cubital crossvein not completely surrounded by brown colouration (Fig. 93). It would be informative to see more material to confirm that this is not merely an extreme variation of *P. platycephala* or *P. microvena*, however.

#### ***P. maculifacies* Camras, 2001**

*Physocephala maculifacies* Camras 2001

**Primary type material examined.** ♂ holotype of *Physocephala maculifacies* Camras, 2001: (1) “Angola (A36) / Chianga / 21.–24.iii.1972”; (2) “Southern / African Exp. / B. M. 1972 -1”; (3) “Holotype ♂ / *Physocephala / maculifacies* / Camras”; coll. NHML.

**Additional material.** ANGOLA: 1♀, 21.–24.iii.1972, Chianga, paratype of *P. maculifacies*, leg. British Museum Expedition, coll. NHML [NHMUK010922096]; TANZANIA: 1♂, 10.iii.1963, Kilimajaru, Weruweru, det. as *P. abyssinica* by Camras 2000, leg. D. J. Greathead, coll. NHML [NHMUK010922099].

A difficult species for which more material is necessary to test the stability of the identification characters given in Key 6.

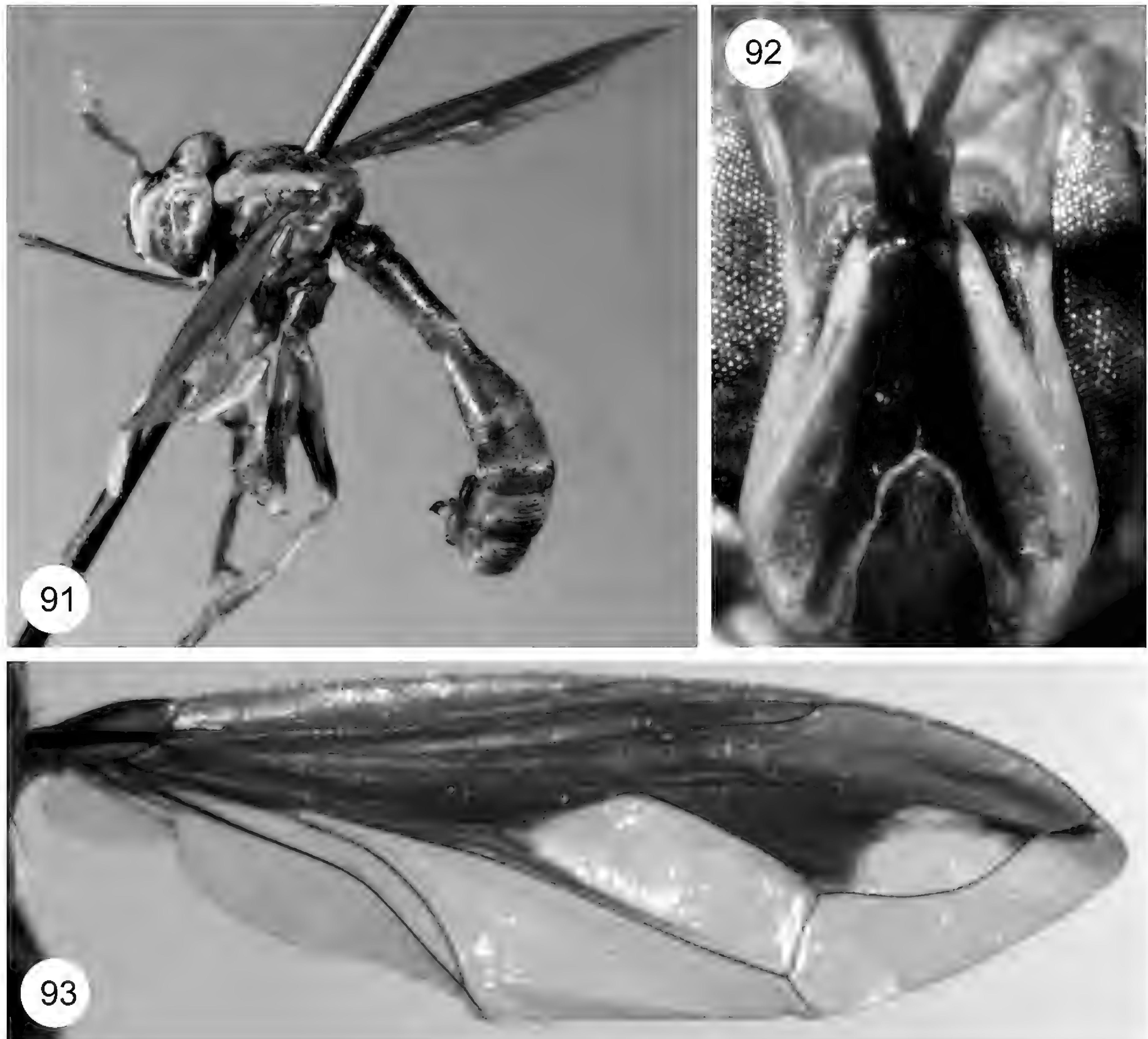
#### ***P. microvena* Brunetti, 1925**

(Figs 94–101)

*Physocephala microvena* Brunetti 1925

= *Pseudophysocephala nigritarsis* Kröber 1939 (**syn. nov.**)





**Figs 91–93.** *Physocephala kroeberi* nom. nov. (♂, Mt. Kenya). **91.** Habitus, lateral view; **92.** Face, anterior view; **93.** Wing, dorsal view.

**Primary type material examined.** 1♀ syntype of *Physocephala microvena* Brunetti 1925: (1) “Syn- / type”; (2) “H. S. Stannus / Zomba. / Nyasaland.”; (3) “Pres. by / Imp. Bur. Ent. / Brit. Mus. / 1924-306”; (4) “*Physo. / microvena* / Brun Type ♀ / Det. E. Brunetti 1924”; (5) “BMNH(E)# / 249157”; coll. NHML.

1♂ syntype of *Physocephala microvena* Brunetti 1925: (1) “Syn- / type”; (2) “H. S. Stannus / Zomba. / Nyasaland.”; (3) “Pres. by / Imp. Bur. Ent. / Brit. Mus. / 1924-306”; (4) “*Physo. / microvena* / Brun / Type ♂ / Det. E. Brunetti 1924”; (5) “BMNH(E)# / 249156”; coll. NHML.

1♂ syntype of *Physocephala microvena* Brunetti 1925: (1) “Syn- / type”; (2) “H. S. Stannus / Zomba. / Nyasaland.”; (3) “Pres. by / Imp. Bur. Ent. / Brit. Mus. / 1924-

306”; (4) “*Physo. / microvena* / Brun / Cotype ♂ / Det. E. Brunetti 1924”; (5) “BMNH(E)# / 249158”; coll. NHML.

1♀ syntype of *Physocephala microvena* Brunetti 1925: (1) “Syn- / type”; (2) “H. S. Stannus / Zomba. / Nyasaland.”; (3) “*Physo. / microvena* / Brun / Cotype ♂ / Det. E. Brunetti 1924”; (4) “BMNH(E)# / 249158”; coll. NHML.

1♀ syntype of *Physocephala microvena* Brunetti 1925: (1) “Syn- / type”; (2) “H. S. Stannus / Zomba. / Nyasaland.”; (3) “Pres. by / Imp. Bur. Ent. / Brit. Mus. / 1924-306”; (4) “*Physocephala / microvena* Brun. / ♂. Cotype. / (Det. E. Brunetti 1924)”; (5) “BMNH(E)# / 249160”; coll. NHML.



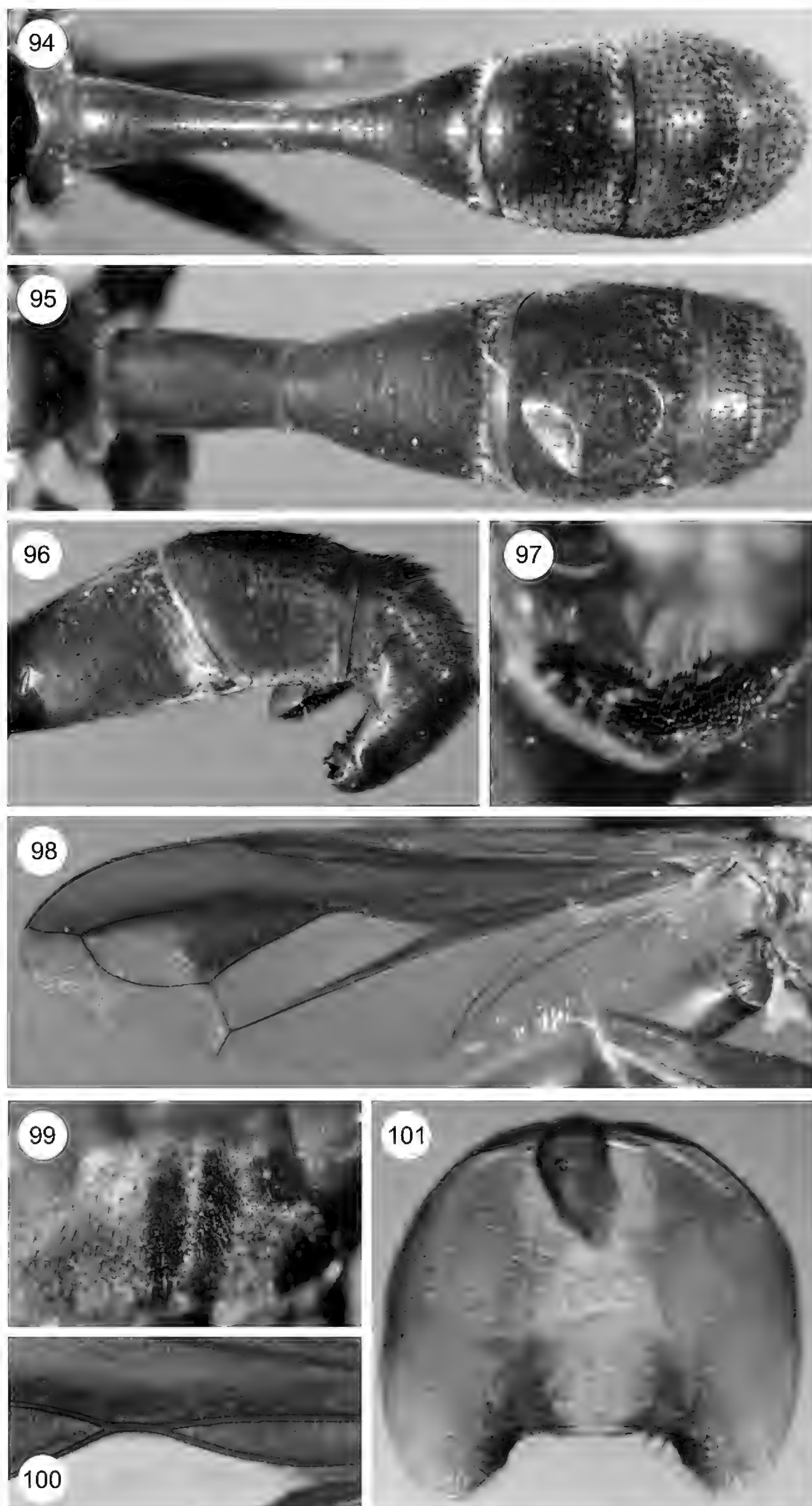
♀ holotype of *Pseudophysocephala nigratarsis* Kröber 1939: (1) “Holo - / type”; (2) “Type”; (3) “Fort Portal / Nyakasura / 24.i.1935 / J. W. Edwards”; (4) “Uganda: / Ruwenzori Range / xii.1934–i.1935. / B. M. E. Afr. Exp. / B. M. 1935-203”; (5) “*Pseudophysocephala / nigratarsis*, Krb. / examined & det. / O. Krober, 1938.”; (6) “*Pseudophysoce- / phala nigri- / tarsis* Krb”; (7) “BMNH(E)# / 249147”; coll. NHML.

**Additional material.** BENIN: 1♀, 1.xii.2011, Lokoli, swamp forest [07°03'40.00"N 02°15'50.00"E], leg. G. Goergen, coll. IITA; BURUNDI: 2♀♀, 5.–12.iii.1953, Bururi, 1800–2000 m [-3.949 29.623], det. as *P. nigratarsis* by Camras 1962, leg. P. Basilewsky, coll. FMNH, MRAC; 1♀, 4.vi.1952, Colline Muramba, Bugoni, Terr. de Muhinga [-2.930 30.357], 1400 m, det. as *P. nigratarsis* by Janssen 1955, leg. F. J. François, coll. ISNB; CAMEROON: 1♂, no date, Neu Kamerun, det. as *P. nigratarsis* by Camras 2000, leg. G. Tessmann, coll. ZMHB; DEMOCRATIC REPUBLIC OF CONGO: 1♀, no date, Elisabethville [Lubumbashi] [-11.664232 27.482626], det. as *P. microvena* by Camras 1962, leg. M. Bequaert, coll. FMNH; 1♀, 10.xi.1928, Ituri, Blukwar, syntype of *P. curta* but not conspecific with designated lectotype, leg. A. Collart, coll. MRAC; 1♀, 12.iv.1953, Kivu, Kitenge, près riv. Ruzizi [-6.896 25.975], leg. J. Verbeke, coll. ISNB; 1♀, 9.iv.1945, Rumangabo, riv. Bugombwa, det. as *P. gigantea* by Janssens 1950, leg. G. F. de Witte, coll. MRAC; 1♀, 29.iii.1954, Secteur Tshiaberimu, riv. Kalivina, affl. Talia Nord, 2350 m [-0.13 29.42], 2350 m, leg. P. Vanschuytbroeck & H. Synave, coll. MRAC; 1♂, 21.–27.viii.1931, Tshibinda [-0.287 28.776], det. as *P. nigratarsis* by Camras 1962, leg. J. Ogilvie, coll. FMNH; KENYA: 1♂, 12.iii.1993, 5 km e Kaimosi, se Kakamega [0.125 34.892], 1750 m, leg. B. Merz, coll. TAUI; 1♂, 10.x.1998, Bungoma [0.5645 34.558], leg. F. Kaplan, A. Freidberg, coll. TAUI; 2♂♂, 12.–13.i.1996, Bungoma [0.5645 34.558], leg. I. Yarom, A. Freidberg, coll. TAUI; 1♀, 8.x.1998, Gilgil [-0.500043 36.326122], leg. F. Kaplan, A. Freidberg, coll. TAUI; 3♂♂ 1♀, 10.x.1998, Kakamega [0.281 34.753], leg. F. Kaplan, A. Freidberg, coll. TAUI; 1♂, 7.–8.ii.2011, Kakamega Forest, 1586 m [0°13'37.2"N 34°52'49.8"E], 1586 m, leg. M. Mei, P. Ceretti, D. Whitmore, coll. PMME; 1♂, 1.–10.ii.2002, Kakamega Isecheno Nature Reserve [0.24'N 34.86'E], 1800 m, leg. Okeka, coll. PMHA; 1♂, 11.–20.i.2003, ditto; 1♂, iv.1969, Karen nr Nairobi, leg. van Someren, coll. NHML [NHMUK010922149]; 1♀, 9.x.1998, Kericho [-0.368726 35.281219], leg. F. Kaplan, A. Freidberg, coll. TAUI; 1♂, 11.–12.iv.1957, Molo, Mau Escarpment, 2150–2200 m, det. as *P. nigratarsis* by Camras 1962, leg. P. Basilewsky, N. Leleup, coll. MRAC; 1♂, ix.1939, Naivasha, det. as *P. nigratarsis* by Camras 1999, leg. H. J. A. Turner, coll. NHML [NHMUK010922138]; 1♀, ix.1939, Naivasha, det. as *P. nigratarsis* by Camras 2000, leg. H. J. A. Turner, coll. NHML [NHMUK010922141];

1♂, 12.iii.1993, near Kaimosi, se Kakamega [0.125606 34.844837], 1750 m, leg. Muhangani, coll. TAUI; 1♀, 16.xi.–22.xii.1998, Rift Valley Province, Mpala research Station [00°19'N 36°53'E], Malaise trap, leg. S. Miller, coll. NMKE; 1♂, 2.–9.i.2000, Western Province, Kakamega Forest, Malaise trap [0°14.13'N 34°51.87'E], leg. R. Copeland, coll. NMKE; UGANDA: 1♂, 22.iv.1966, 20 miles e Mubende, leg. D. J. Greathead, coll. NHML [NHMUK010922147]; 1♂, 19.x.1958, Kawanda, det. as *P. nigratarsis* by Camras 2000, [collector unknown], coll. NHML [NHMUK010922137]; 1 specimen, xii.1934–i.1935, Ruwenzori Range, det. as *P. nigratarsis* by Camras 2000, leg. B. M. E. Africa Expedition, coll. NHML [NHMUK010922140]; 1♂, 20.iii.2012, Rwenzori Gebirge, Nyakalengila [N002100 E300149], 1705 m, leg. Oehlke, coll. PASS; 1♂, 16.xi.1949, Shangugu [= Cyangugu] [-2.483333 28.896667], 1460 m, det. as *P. platycephala* by Janssen 1954, leg. F. J. François, coll. ISNB; ZIMBABWE: 1♀, 2.–6.xii.2015, Chirinda Forest, Mt. Selinda [20°25'S 32°43'E], 1000 m, leg. J. Halada, coll. CULSP; 1♂, 18.vi.1964, n Vumba [= Bvumba] [-19.093432 32.740631], det. as *P. microvena* Camras 2000, leg. D. Cookson, coll. FMNH; 2♂♂, 4.vii.1964, n Vumba [= Bvumba] [-19.093432 32.740631], det. as *P. microvena* Camras 2000, leg. D. Cookson, coll. FMNH; 1♀, 18.vii.1964, n Vumba [= Bvumba] [-19.093432 32.740631], det. as *P. microvena* by Camras 2000, leg. D. Cookson, coll. FMNH; 1♀, 8.x.1964, n Vumba [= Bvumba] [-19.093432 32.740631], det. as *P. microvena* by Camras 2000, leg. D. Cookson, coll. FMNH; 1♂, 20.ii.1965, n Vumba [= Bvumba] [-19.093432 32.740631], det. as *P. microvena* Camras 2000, leg. D. Cookson, coll. FMNH; 1♀, 8.v.1965, n Vumba [= Bvumba] [-19.093432 32.740631], det. as *P. microvena* by Camras 1999, leg. D. Cookson, coll. FMNH; 1♀, 8.v.1965, n Vumba [= Bvumba] [-19.093432 32.740631], det. as *P. microvena* by Camras 2000, leg. D. Cookson, coll. FMNH; 1♀, v.1932, Xmas Pas, Umtali [= Christmas Pass near Mutare], leg. J. Ogilvie, coll. NHML [NHMUK010922146]; 1♂, v.1932, ditto [NHMUK010922148].

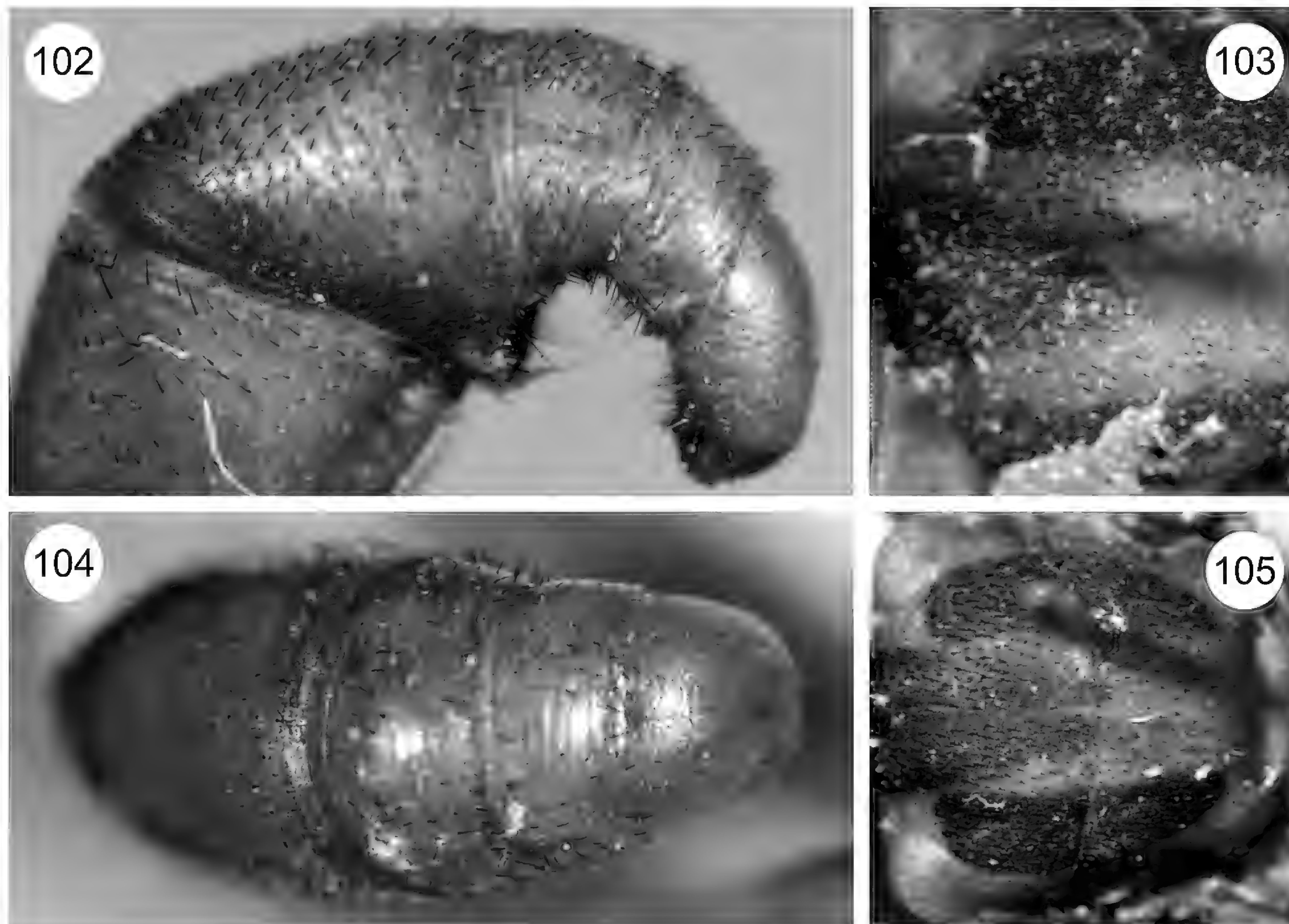
Most *P. microvena* specimens characteristically have veins M and  $R_{4+5}$  fused, thus lacking any radial-medial crossvein (Figs 98, 100). A minority of specimens do have a very short radial-medial crossvein present, however, and a reduced crossvein rm may also occur occasionally in specimens of other species, causing complications in identification. Females of *P. microvena* are easily identified by the short, broad theca (Fig. 97) and short abdominal segments (Fig. 96), with confusion only really likely with *P. pseudomicrovena*, which may be conspecific. Conversely, males of *P. microvena* are extremely difficult to identify reliably and could be easily confused with males of other species-groups and also with males of *P. constricta* where these also have a reduced radial-medial crossvein. Where present, the distance between





**Figs 94–101.** *Physocephala microvena* Brunetti, 1925. **94.** ♂ abdomen, dorsal view (♂, n Vumba); **95.** ♀ abdomen, dorsal view (♀, n Vumba); **96.** ♀ abdomen, lateral view (♀, n Vumba); **97.** ♀ theca, ventral view (♀, n Vumba); **98.** Wing, dorsal view (♀, n Vumba); **99.** Scutum with dusting stripes, anterodorsal view (♂, n Vumba); **100.** Completely reduced radial-medial crossvein, dorsal view (♀, n Vumba); **101.** ♂ epandrium, dorsal view (♂, Bumgoma).





**Figs 102–105.** *Physocephala platycephala* (Loew, 1853). **102:** tip of ♀ abdomen, lateral view (♀, Worcester); **103.** ♀ scutum, dorsal view (♀, Worcester); **104.** Tip of ♀ abdomen, dorsal view (♀, Worcester); **105.** ♂ scutum, dorsal view (♂, Clanwilliam dam).

the two short dark submedial stripes in the microtrichial dusting on the anterior scutum may be the best character for separating *P. constricta* and *P. microvena*, these being separated by a wider medial dusted stripe in the former (Fig. 81) than in the latter (Fig. 99).

As mentioned by Camras (2001) there are several intermediates between typical *P. microvena* and *P. nigratarsis*. Therefore, *Pseudophysocephala nigratarsis* Kröber, 1939 is herewith placed as a junior synonym of *Physocephala microvena* Brunetti, 1925 (**syn. nov.**).

***P. platycephala* (Loew, 1853)**

*Conops platycephalus* Loew 1853  
(Figs 102–105)

**Material.** SOUTH AFRICA: 1♂, 3.–7.x.1988, Cape Province, Clanwilliam Dam [32°11'30"S 18°53'42"E], on flowers of *Aspalathus desertorum* Bol., leg. F. W. Gees, S. K. Gees, coll. AMGS; 1♀, ix.1928, Cape Province, Worcester, det. as *Physocephala* spec. by Kröber 1938, det. as *P. platycephala* by Camras 2000, leg. R. E. Turner, coll. NHML [NHMUK010922130].

While the female of *P. platycephala* is easily recognised by the obvious shape of the postabdomen and theca (Figs 102, 104), males are more problematic. We doubt that males can be reliably identified using the colour pattern of the scutum as proposed by Camras (2001) and as described in Key 6. Figs 103 & 105 show that the black spots on the scutum are less distinctly separated in males (Fig. 105) compared to females (Fig. 103), and may perhaps sometimes become fused. Perhaps males of this rare species – only two female specimens are known – have therefore previously been misidentified as other species.

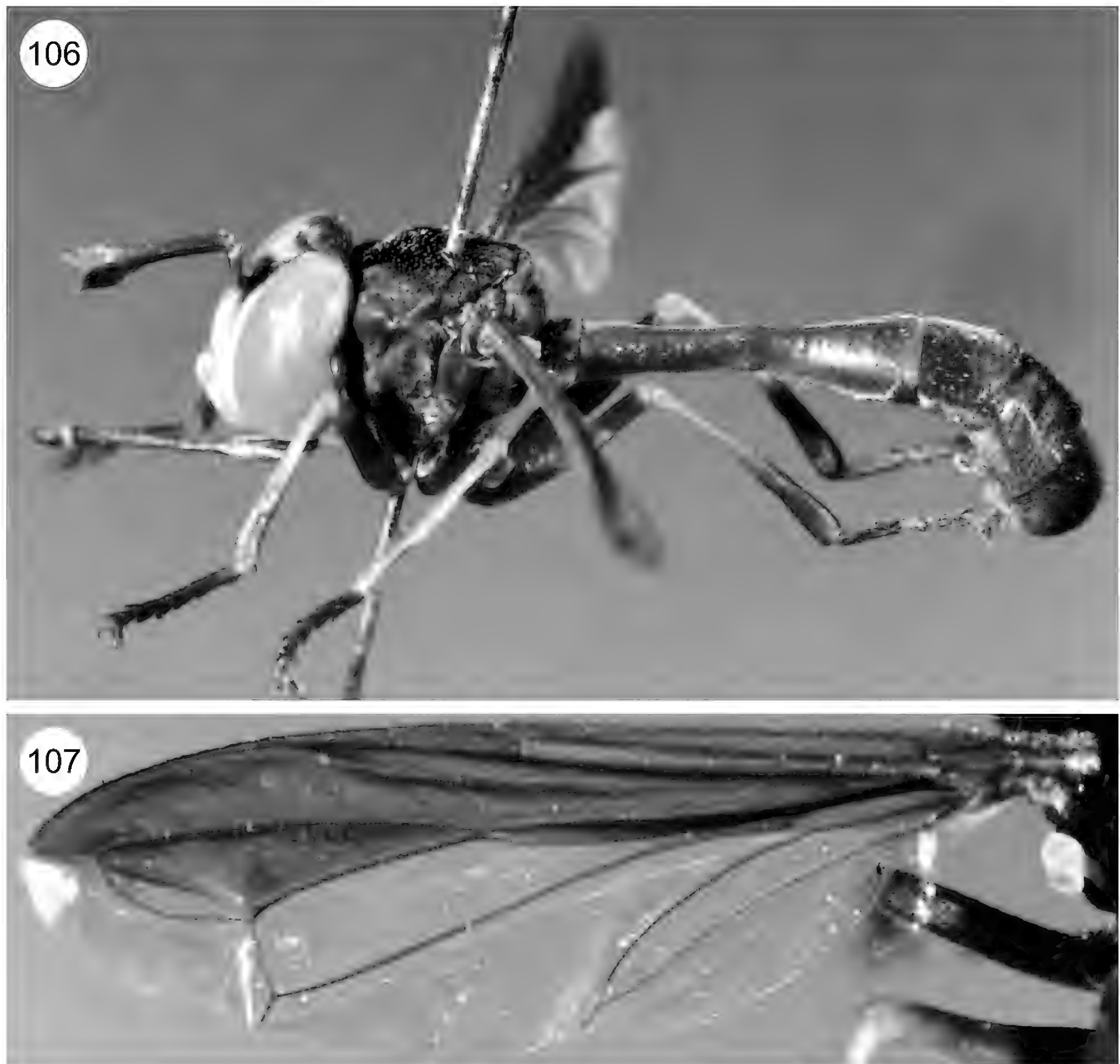
***P. pseudomicrovena* Kröber, 1939**

(Figs 106–107)

*Physocephala pseudomicrovena* Kröber 1939

**Primary type material examined.** ♂ lectotype of *Physocephala pseudomicrovena* Kröber, 1939 designated by Camras (1962): (1) “♂ / Holotypus”; (2) “Musée du Congo / Tanganyka-Moero : / Nyunzu - I - II - 1934/ De Saeger”; (3) “R. DÉT / O / 2992”; (4) “*Physocephala* ♂ / *microvena* Brun. / var. / det. Kröber 1935”; (5) “RMCA





**Figs 106–107.** *Physocephala pseudomicrovena* Kröber, 1939. **106.** Habitus, dorsolateral view (♂, Athiémé); **107.** Wing, dorsal view (♂, Athiémé).

ENT / 000012181”; (7) “Type ♂ / *Physocephala* / *pseudomicrovena* / Kröber”; (7) “designated by / Camras, 1962”; coll. MRAC.

**Additional material.** BENIN: 1♂, viii.2006, Athiémé [06°14'20.00"N 01°40'00.00"E], leg. G. Goergen, coll. IITA; 2♀♀, viii.2006, Athiémé [06°14'20.00"N 01°40'00.00"E], sweep netting, leg. G. Goergen, coll. IITA; 1♀, v.2006, Lokossa, sweep netting, leg. G. Goergen, coll. IITA.

The lectotype is in poor condition, with the antennae missing and a broken abdomen almost completely covered with glue. All of the characters which can be seen fit well to the concept of the species as given in Key 6, however. Nevertheless, this species is only poorly differentiated from *P. microvena*, and it may easily be no more than a dark morph of that species. On the other hand, all of the specimens available to us can be distinguished with the characters given in Key 6 and therefore the species is here accepted as valid.



### *Physocephala pilitarsis* species-group

This group is identical to the *Pseudophysocephala pilitarsis* species-group of Camras (2001). Contrary to Camras (2001), however, it is not straightforwardly identified because the main character he used – a large hyaline area between the vena spuria and media in cell  $r_{4+5}$  – also occurs in some other *Physocephala* species-groups. Females belonging to this group are relatively easy to recognise by the theca, and the chaetotaxy and shape of the tarsi (Key 1). Males are more difficult to identify, however, and only careful examination of several characters in combination will rule out placement in other groups. In addition, species identification of males is so far based mainly on colouration characters, which may be variable. There has not been enough material available to begin looking at the male genitalia. All members of this species-group are restricted to the Afrotropical Region.

#### Key 7 – Identification of the *Physocephala pilitarsis* species-group

1. Reddish-brown species, scutum with three black stripes, scutellum reddish-brown, abdomen mainly reddish-brown; ♀ fore tarsi wide and bare, lacking any long setulae which are curled apically [based on the original description only] ..... *P. rufa* (Camras, 2001)
  - Black to brown species, scutum mainly black, lacking distinct stripes, scutellum black, abdomen with at most tergites 1–3 orange-brown; ♀ fore tarsi often with unusual characters such as curled setulae ..... 2
2. Basal cell and basal medial cell dark and completely covered with microtrichia (Fig. 118); radial-medial crossvein sometimes quite short and the hyaline area posterior to vena spuria in cell  $r_{4+5}$  sometimes indistinct (Fig. 118); ♀ fore tarsus and middle tarsus with long setulae which are curled apically (Figs 114, 116); ♀ theca triangular and adpressed to abdomen (Fig. 115); ♀ sternite 6 with broad field of black setae which is concave posteriorly (Fig. 115) ..... *P. pilitarsis* Kröber, 1936
  - Basal cell and basal medial cell hyaline, and at least partly lacking microtrichia; radial-medial crossvein sometimes quite short but the hyaline area posterior to vena spuria in cell  $r_{4+5}$  is always distinct; ♀ fore tarsus may have long setulae but these are not curled apically; ♀ theca and ♀ sternite 6 different ..... 3
3. Pulvilli spine-like (Fig. 120) ..... *P. spinipes* (Camras, 2001)
  - Pulvilli not spine-like, but normally developed ..... 4
4. Cells  $r_1$  and  $r_{2+3}$  completely dark brown, costal cell never hyaline but sometimes paler than cell  $r_1$  (Fig.

113); ♀ fore tarsus and middle tarsus not obvious widened and lacking outstandingly long setulae (Fig. 109); ♀ hind tibia with extremely short tarsomeres (Figs 111, 112); ♀ theca shown in Fig. 110 ..... *P. nitida* (Kröber, 1915)

- Cells  $r_1$  and  $r_{2+3}$  more or less hyaline, never both completely tinged dark brown, costal cell sometimes hyaline; ♀ fore tarsus with or without long setulae; ♀ hind tibia, hind tarsomeres and theca different ..... 5
5. Costal cell pigmented but slightly paler than cell  $r_1$ ; cells  $r_{2+3}$  and  $r_{4+5}$  apically hyaline, with base contrasting darker; ♀ fore and middle tarsi obvious shorter than tibiae; fore tarsus with characteristic long setulae: at apex with one pair of forward-directed and strongly incurved setulae, and basally with two pairs of strongly back-curved setulae; ♀ sternite 6 with a broad field of black, dispersed setae ..... *P. tetratarsata* (Camras, 2001)
    - Wing with different markings; ♀ fore and middle tarsi different; ♀ sternite 6 different ..... 6
  6. Cell  $r_1$  completely dark brown, cell  $r_{2+3}$  mostly dark brown and only slightly paler apically; abdomen completely black; ♀ theca with two patches of 6–7 strong black setae; sternite 6 with two distinct lateral fields of dense black setae and on each sits a pair of very close-set, long and strong black setae; ♀ fore tarsus not obviously widened, and lacking long setulae which equal the tarsus width ..... *P. basilewskyi* (Camras, 1962)
    - Cell  $r_1$  mainly hyaline, cell  $r_{2+3}$  at most slightly infuscated dark brown (Fig. 125); tergites 2–3 at least partly orange-brown (Fig. 122); ♀ theca and sternite 6 lacking any fields of setae or long strong setae, but with a large plate which has sparse fine setulae (Fig. 124); ♀ fore tarsus obviously widened and with long black setulae which equal the tarsus width (Fig. 123) ..... *P. vitripennis* Curran, 1928

#### *P. basilewskyi* (Camras, 1962)

*Pseudophysocephala basilewskyi* Camras 1962

**Primary type material examined.** ♀ holotype of *Pseudophysocephala basilewskyi* Camras, 1962: (1) “♀ / Holotypus”; (2) “Coll. Mus Congo / Kib.-Ituri : Irumu / 18/XII-1952 / P. Basilewsky”; (3) “Holotype ♀ / *Pseudophysocephala* / *basilewskyi* / Camras”; (4) “RMCA ENT / 000012176”; coll. MRAC.

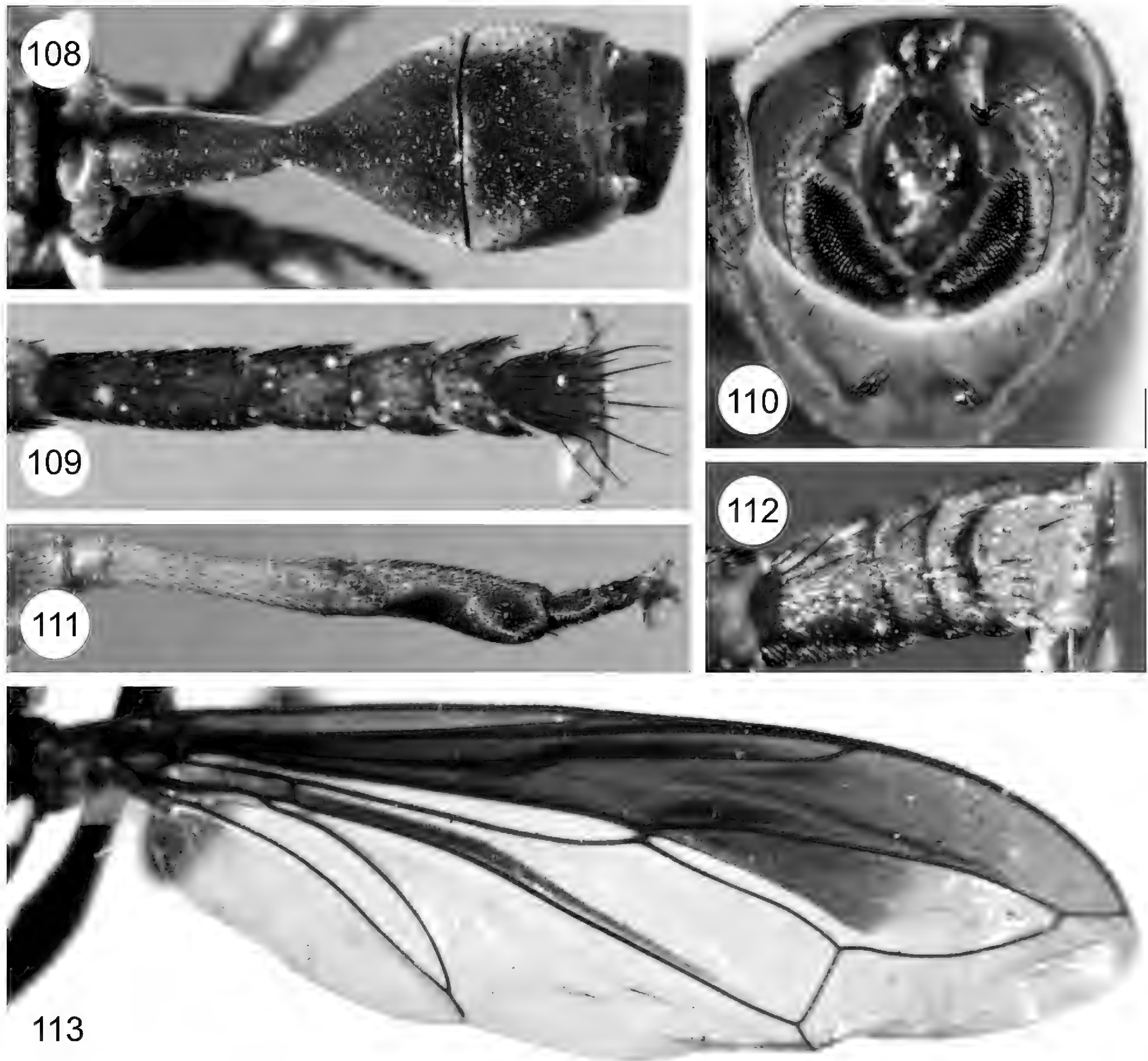
#### *P. nitida* (Kröber, 1915)

(Figs 108–113)

*Conops nitidus* Kröber 1915

**Primary type material examined.** ♂ holotype of *Conops nitidus* Kröber 1915f: (1) “Togo / Bismarckburg / 2.–





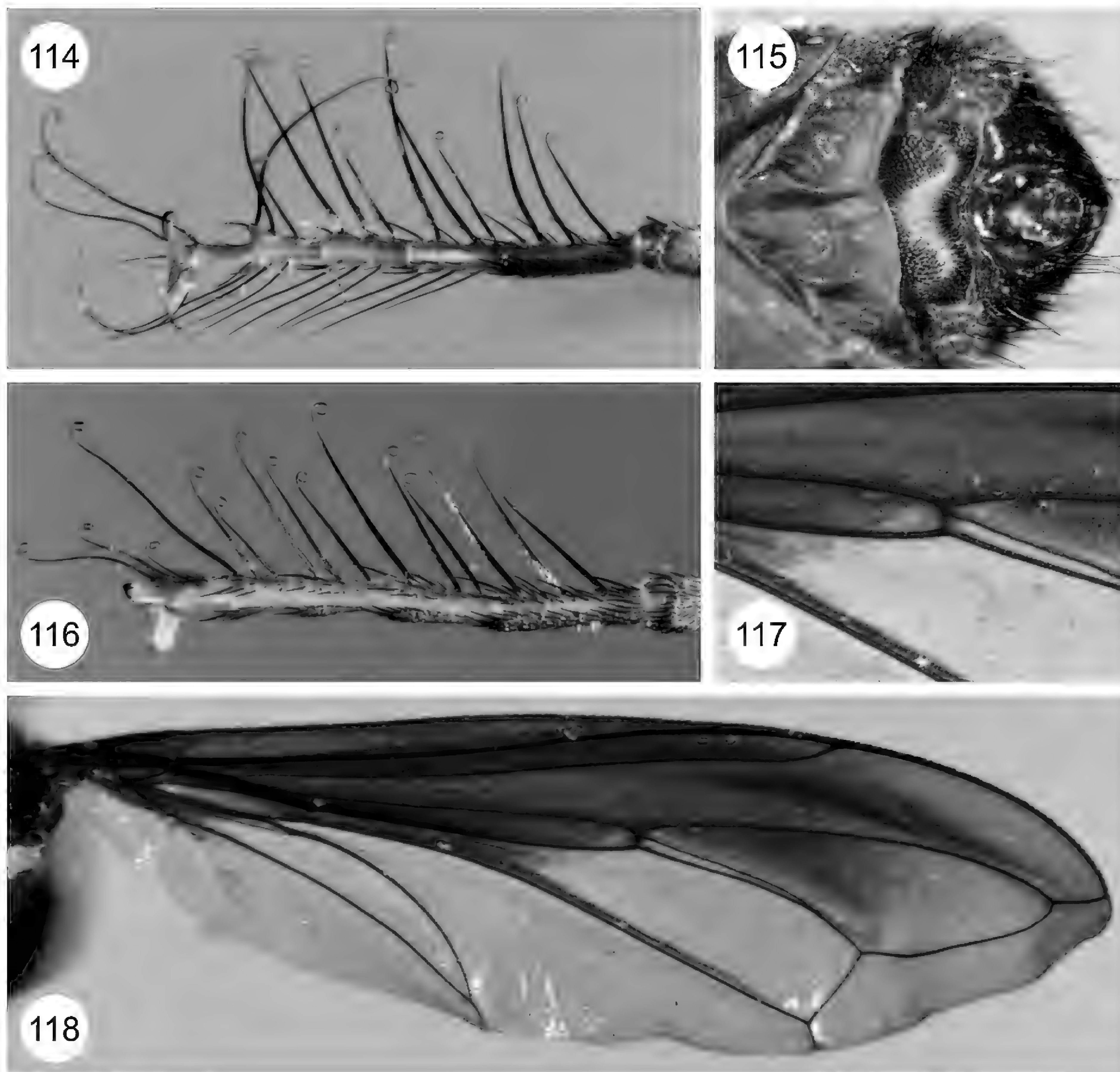
**Figs 108–113.** *Physocephala nitida* (Kröber, 1915) (♀, Kloto forest). **108.** ♀ abdomen, dorsal view; **109.** ♀ fore tarsi, dorsal view; **110.** ♀ theca, ventral view; **111.** ♀ hind tibia and hind tarsi, lateral view; **112.** ♀ hind tarsi, dorsal view; **113.** Wing, dorsal view.

18.vi.93 / L. Conradt S.”; (2) “*Conops* ♂ / *nitidus* Kröb/ O. Kröber det. 1914”; (3) “Cotype”; (4) “Zool. Mus. Berlin”; (5) “*Pseudophysocephala* / *nitidus* / Kröber / det. Camras, 2000”; coll. ZMHB.

**Additional material.** BENIN: 1♂, x.2008, Ahozon, forest area [06°22'57.59"N 02°9'15.92"E], leg. G. Goergen, coll. IITA; 1♀, 26.iii.2013, Dangbo, sacred forest, leg. G. Goergen, coll. IITA; KENYA: 1♂, 12.–26.ii.2005, Nyanza Province, Ungoye Field Station [0°36.91'S 34°05.52'E], 1147 m, leg. R. Copeland, coll. NMKE;

1♂, 27.ii.–6.iii.2005, ditto; TANZANIA: 1♀, 1.vi.–4.vii.1893, Bismarckburg [= Kasanga], det. as *P. nitida* by Kröber 1914 and Camras 2000, wrongly interpreted as female syntype, leg. L. Conradt S., coll. ZMHB; TOGO: 1♂, 26.i.2016, Dzobégan, monastery [7°14'22.07"N 0°41'58.64"E], leg. G. Goergen, coll. IITA; 1♂, ix.2006, Kloto, forest area [6°57'31.66"N 0°34'29.75"E], leg. G. Goergen, coll. IITA; 1♂, viii.2008, ditto; 1♂, i.2005, ditto; 1♀, vi.2008, ditto; 1♀, x.2016, ditto.





**Figs 114–118.** *Physocephala pilitarsis* Kröber, 1936 (♀, Kakamega forest). **114.** ♀ fore tarsus, ventral view; **115.** ♀ postabdomen, ventral view; **116.** ♀ middle tarsus, lateroventral view; **117.** Radial-medial crossvein, dorsal view; **118.** Wing, dorsal view.

***P. pilitarsis* Kröber, 1936**

(Figs 114–118)

*Physocephala pilitarsis* Kröber 1936

= *Pseudophysocephala ugandae* Kröber 1939, junior homonym of *Physocephala ugandae* Kröber, 1915

**Primary type material examined.** ♀ holotype of *Physocephala pilitarsis* Kröber, 1936: (1) “Ph. Type / *pilitarsis*”; (2) “Musée du Congo / Ubangi: Nzali / 3/4-II-1932 / H. J. Brédo”; (3) “R. DÉT / N / 2992”; (4) “*Physocephala* / *pilitarsis* Krb. / det. Kröber 1935”; (5) “Typus”; (6) “RMCA ENT / 000012180”; coll. MRAC.

♂ holotype of *Pseudophysocephala ugandae* Kröber, 1939: (1) “Holo- / type”; (2) “Mpanga Forest / c 4,000 ft / F. W. Edwards”; (3) “Uganda: / Ruwenzori Range. /

xii.1934–i.1935. / B. M. E. Afr. Exp. / B: M. 1935-203.”; (4) “*Pseudophysocephala* / *ugandae* Kröb. / examined & det. / O. Kröber 1938.”; (5) “*Pseudophysocephala* / *ugandae* / Krb”; (6) “Type”; (7) “*Pseudophysocephala* / *pilitarsis* / Kröber / det. Camras, 2000”; coll. NHML.

**Additional material.** CENTRAL AFRICAN REPUBLIC: 1♂, 14.vi.2009, 150 km nww Mbaiki [04°05'N 17°02'E], 620 m, leg. J. Halada, coll. CULSP; 1♀, 2.v.2010, 20 km nne Mbaiki [03°04'N 18°00'E], 450 m, leg. J. Halada, coll. CULSP; 1♂, 9.xi.2012, 40 km e of Bambio [3°60'N 17°12'E], 500 m, leg. J. Halada, coll. CULSP; 1♂, 9.xii.2008, 50km ne Bambio [03°59'N 17°11'E], 450 m, leg. J. Halada, coll. CULSP; 3♂♂, 4.xii.2010, 60 km w Banibo [3°50'N 16°44'E], 630 m,



leg. J. Halada, coll. CULSP; 1♂, 24.–28.xi.2010, 70 km nne Bangui [04°57'N 18°46'E], 445 m, leg. J. Halada, coll. CULSP; DEMOCRATIC REPUBLIC OF CONGO: 1♂, xii.1923, Katombe, Katanga, det. as “? *abyssinica*” by Brunetti 1925, det. as *P. pilitarsis* by Camras 1962, leg. Bequaert, coll. MRAC; 1♂, viii.1932, Lulua, Kapan-ga, det. as *P. “abyssinica* Krb var.” by Kröber 1935, leg. F. G. Overlaet, coll. MRAC; 1♂, xi.1932, Lulua, Kapan-ga, det. as *P. “abyssinica* Krb var.” by Kröber 1935, leg. F. G. Overlaet, coll. MRAC; 1♂, 1.iv.1937, Terr. Lisala, det. as *P. pilitarsis* by Camras 1962, leg. Leontovich, coll. MRAC; EQUATORIAL GUINEA: 1♀, 16.–31.viii.1906, Alén, Benitogebiet, det. as *P. pilitarsis* by Camras 2000, leg. G. Tessmann, coll. ZMHB; 1♀, 1.–15.xi.1906, Alén, Benitogebiet, det. as *P. pilitarsis* by Camras 2000, leg. G. Tessmann, coll. ZMHB; 2♂♂, vi.–viii.1908, Uelleburg, det. as *P. pilitarsis* by Camras 2000, leg. G. Tessmann, coll. ZMHB; KENYA: 1♂, 13.–27.viii.2006, Western Province, Kakamega Forest near Rondo Guest House [0.22767°N 34.88533°E], 1630 m, Malaise trap set across small permanent stream, leg. R. Copeland, coll. NMKE; 1♀, 3.–17.xii.2006, ditto; 1♀, 13.–27.viii.2006, ditto; 1♂, 12.–19.iii.2000, Western Province, Kakamega Forest, Malaise trap [0°14.13'N 34°51.87'E], leg. R. Copeland, coll. NMKE; 1♂, 28.viii.–4.ix.1999, ditto; 1♂, 2.–9.i.2000, ditto; 1♀, 20.–27.xi.1999, ditto; 2♀♀, 17.–24.vii.1999, ditto; 1♀, 13.–20.ii.2000, ditto; 2♀♀, 11.–18.ix.1999, ditto; 2♀♀, 3.–10.vii.1999, ditto; 1♀, 21.–28.v.2000, ditto; UGANDA: 1♂, vi.1912, Kawanda, det. as *P. pilitarsis* by Camras 2000, leg. D. J. Greathead, coll. NHML [NHMUK010922154]; 1♂, 2.viii.1962, Mabira Forest, det. as *P. pilitarsis* by Camras 2000, leg. D. J. Greathead, coll. NHML [NHMUK010922155].

### ***P. rufa* (Camras, 2001)**

*Pseudophysocephala rufa* Camras 2001

No material of this species has been seen by us. Only the female holotype is known, recorded from Malawi (Mulanje Mountain, Nr. Likabula) at 1500m.

### ***P. spinipes* (Camras, 2001)**

(Figs 119–121)

*Pseudophysocephala spinipes* Camras 2001

**Primary type material examined.** ♀ holotype of *Pseudophysocephala spinipes* Camras 2001: (1) “Tanganyika / Amani / 1957 / J. G. Halcrow / in thick bush”; (2) “C. I. E. Coll. / NO 15485”; (3) “*Pseudophysocephala* / sp. ? / Det. R. L. Coe. 1958”; (4) “Pres. by / Com Inst Ent / B M 1969-3”; (5) “Holotype ♀ / *Pseudophysocephala* / *spinipes* / Camras”; coll. NHML.

**Additional material.** KENYA: 1♀, 23.ix.2005, Kakamega Forest, Yala River [0°13'N 34°53'E], 1450 m, leg. A. Freidberg, coll. TAUI.

### ***P. tetratarsata* (Camras, 2001)**

*Pseudophysocephala tetratarsata* Camras 2001

**Primary type material examined.** ♀ holotype of *Pseudophysocephala tetratarsata* Camras 2001: (1) “Yaoundé Cam. / Nkolbisson / Nonvll. X 1974”; (2) “parasitizing 6”; (3) “61a”; (4) “C. I. E. Coll. / A. 7811”; (5) “Pres by / Comm Inst Ent / B M 1975-1”; (6) “Holotype ♀ / *Pseudophysocephala* / *tetratarsata* / Camras”; (7) “*Pseudophysocephala* / *tetratarsata*” and on underside of this label “*Pseudophyso.* / BM. Mus. From. / Yaounde Cam”; coll. NHML.

Below the holotype is a large label with additional information: “Following and ovipositing on bees which were collecting sap flowing from Scolyid entrance holes in felled trees. Each was following a bee flying immediately behind it. When a *Physocephala* managed to approach closely a bee the fly deposited an egg on its body with an extreme rapidity and I could establish later that the egg remained attached to the tegument of the bee. Dr. Guido Nonveiller in letter 6.4.76 to K. M. Harris. C. I. E.” [Commonwealth Institute of Entomology].

### ***P. vitripennis* Curran, 1928**

(Figs 122–125)

*Physocephala vitripennis* Curran 1928

= *Physocephala intermedia* Kröber 1936 (**syn. nov.**)

= *Conops bouvieri* Séguéy 1936 (**syn. nov.**)

= *Pseudophysocephala meii* Camras 2001 (**syn. nov.**)

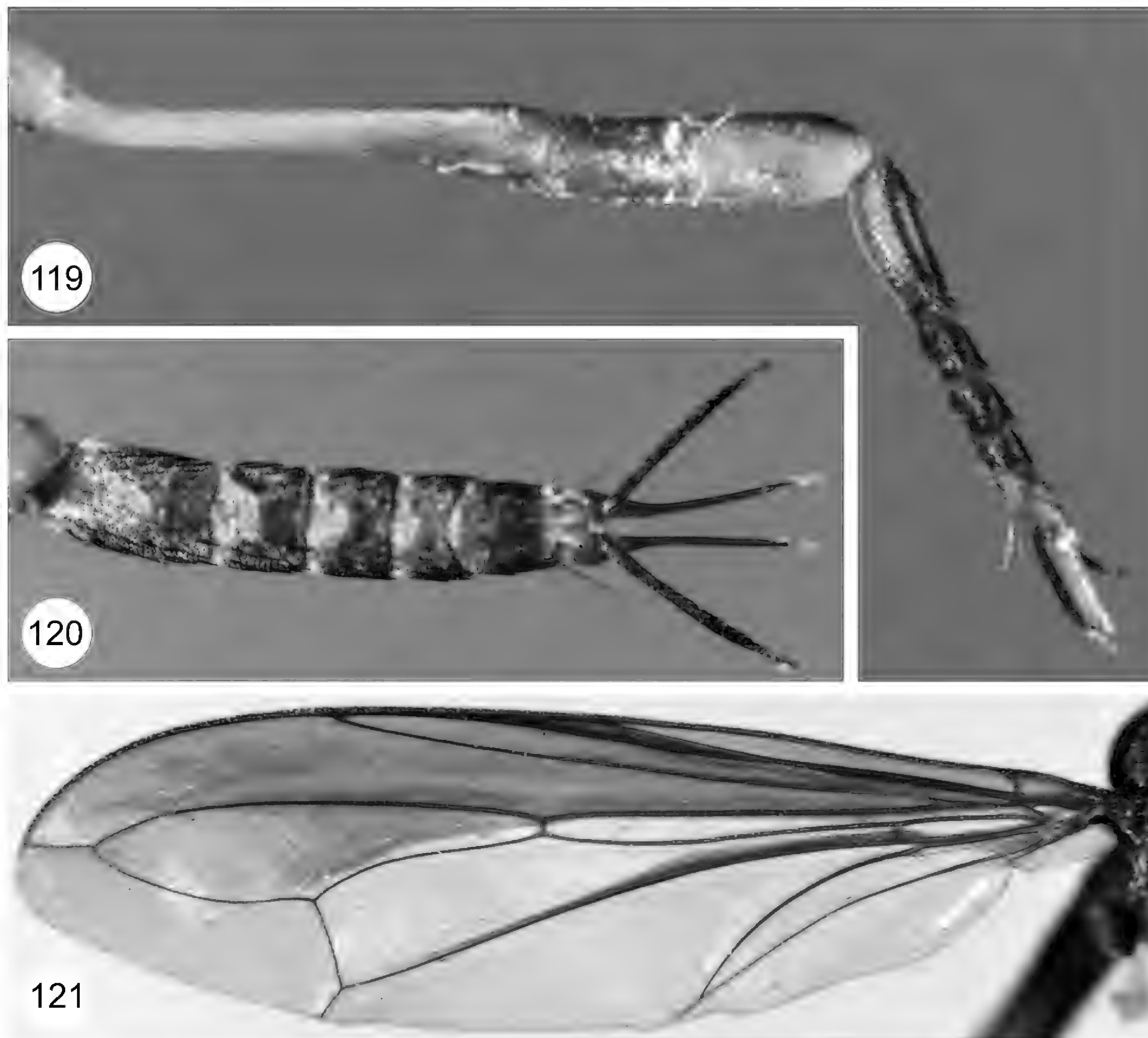
= *Pseudophysocephala acroschista* sensu Camras (2001), nec Speiser, 1911

**Primary type material examined.** ♂ holotype of *Physocephala intermedia* Kröber, 1936: (1) “Ph. Type ♂ / *intermedia*”; (2) “Musée du Congo / Ubangi: Nzali / 3/4-II-1932/ H. J. Brédo”; (3) “R. DÉT / Z / 2992”; (4) “*Physocephala* ♂ / *intermedia* Krb. / det. Kröber 1935”; (5) “Type”; (6) “RMCA ENT / 000012179”; coll. MRAC.

♀ holotype, ♂ paratype (pinned on one needle) of *Pseudophysocephala meii* Camras 2001: (1) “République de Guinea PNHN5 / 10°16'43"N 10°26'02"W / Faranen, Sidakoro, mangor, / 29.XII.1995, leg. M. Mei”; (2) “Holotype ♀ and ♂ / *Pseudophysocephala* / *meii* / Camras”; (3) [glued male abdomen]; (4) “*Pseudophysocephala* / cf *vitripennis* Curran / M. Mei det. 1997”; (5) “*Pseudophysoc* / *meii*”; coll. FMNH.

**Additional material.** BENIN: 1♂, 20.iii.2011, Niaouli, forest area [06°44'3.08"N 02°8'2.59"E], leg. G. Goergen, coll. IITA; 1♂, 2.ii.2014, Niaouli, forest area [06°44'3.08"N 02°8'2.59"E], sweepnetting, leg. G. Goergen, coll. IITA; 2♂♂, xi.2016, Sérrou, forest area [09°40'03.00"N 01°41'50.00"E], leg. G. Goergen, coll. IITA; DEMOCRATIC REPUBLIC OF CONGO: 1 specimen, 18.x.1945, Tshuapa, Flandria, det. as *P. intermedia*





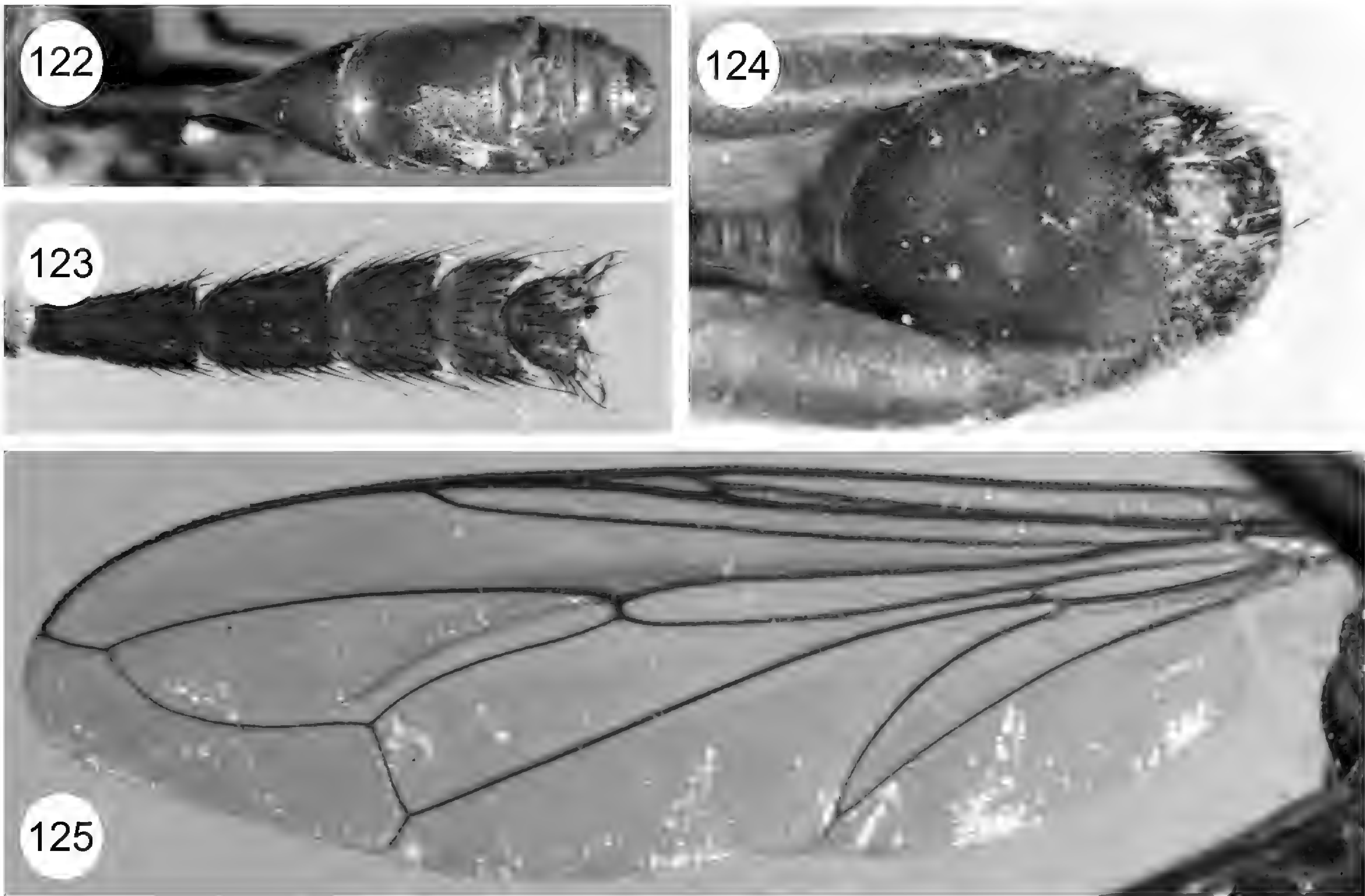
**Figs 119–121.** *Physocephala spinipes* (Camras, 2001) (♀, Kakamega forest). **119.** ♀ hind tibia and tarsi, lateral view; **120.** Middle tarsi, dorsal view; **121.** Wing, dorsal view.

by Camras 1962, leg. P. Hulstaert, coll. MRAC; 2♂♂, no date, Ville Malela, Chief Casende [5,40S 23,45E], det. as *P. acroschista* by Camras 2000, det. as *P. intermedia* by Camras 1962, leg. J. Bequaert, coll. FMNH; GHANA: 1♂, 9.ix.1947, Kumasi, paratype of *P. meii*, leg. J. Bowden, coll. NHML [NHMUK010922153]; NIGERIA: 2♂♂, xii.1998, Ibadan, IITA, sweeping net in forest, leg. G. Goergen, coll. IITA; 1♀, 30.i.1988, Ibadan, IITA, leg. G. G. M. Schulten, coll. RMNH; 1♀, 3.ii.2000, Ibadan, IITA, on mud at forest margin, leg. G. Goergen, coll. IITA; SIERRA LEONE: 1♂ 1♀, 28.xi.1993, 5 km w Kabala, swept along road [09°35'N 11°35'W], leg. L. Cederholm, R. Danielsson & R. Hall, coll. MZLU; UGANDA: 1♀, 16.i.1966, nr. Entebbe, paratype of

*P. meii*, attacking *Apis*, leg. D. J. Greathead, coll. NHML [NHMUK010922152].

Camras (1962b, 2001) was the only author to distinguish four very similar species of the *pilitarsis* group: *P. vitripennis* (Curran, 1928), *P. intermedia* (Kröber, 1936) (as *P. acroschista sensu* Camras (2001) *nec* Speiser, 1911), *P. bouvieri* (Séguy, 1936) and *P. meii* Camras, 2001. He used characters of wing colouration, relative length of tarsomeres and extent of dusting on the postpronotum to segregate these, but all of these characters are variable and the four taxa intergrade. There is little consistent difference in the female theca or tarsi between these taxa. The holotypes of *P. intermedia* and *P. meii* were avail-





**Figs 122–125.** *Physocephala vitripennis* (Curran, 1928). **122.** ♀ abdomen, dorsal view (♀, w Kabala); **123.** ♀ fore tarsi, dorsal view (♀, w Kabala); **124.** ♀ theca, ventral view (♀, w Kabala); **125.** Wing, dorsal view (♀, Ibadan).

able to us but the holotype of *P. bouvieri*, which should be in Muséum National d’Histoire Naturelle, Paris, but which was not included in the list of material available there (GBIF 2019), could not be investigated. These four species are herewith treated as synonyms: *Physocephala vitripennis* Curran, 1928 = *Physocephala intermedia* Kröber, 1936 (**syn. nov.**) = *Physocephala* [*Conops*] *bouvieri* Séguy, 1936 (**syn. nov.**) = *Physocephala* [*Pseudophysocephala*] *meii* Camras, 2001 (**syn. nov.**).

***Physocephala pubescens* species-group**

Our *pubescens*-group equates to the *Pseudophysocephala pubescens* species-group of Camras (2001). This group is easily recognised by the distinct setae on the mediotergite and several other subtle characters as summarised in Key 1. Key 8 below, and the interpretation of the species presented here, is based mainly on the key and descriptions of Camras (2001). All members of this group are restricted to the Afrotropical Region.

**Key 8 – Identification of the *Physocephala pubescens* species-group**

- 1. Frons with numerous short setulae (e.g. Fig. 129), or least laterally with some setulae additional to those on vertex; scutum and mediotergite with short setae only, shorter than diameter of a tibia (e.g. Fig. 148). ..... **2**
  - Frons lacking setulae, setulae only present on vertex; scutum and mediotergite with long setae, longer than diameter of a tibia (e.g. Fig. 141)..... **5**
- 2. Tibiae lacking or with only very indistinct rows of black setulae (e.g. Fig. 127); setulae on frons and face obvious and widely distributed, some of them inside the facial grooves and on the facial ridges (e.g. Figs 128, 129)..... **3**
  - Tibiae dorsally with distinct rows of black setulae (e.g. Fig. 140); no setulae in facial grooves or on facial ridges ..... **4**
- 3. Very long, fine and dense setulae all over; long setulae on hind femur are especially obvious. Long setulae all over frons (longer than the diameter of hind tibia), and on abdomen. ***P. hirta* (Kröber, 1939)**



- Vestiture of fine setulae much less long and dense. Very few setulae anywhere longer than diameter of hind tibia..... ***P. barbata* (Camras, 2001)**
  
- 4. Maximum length of apical aristomere about twice maximum length of projection of basal aristomere (Kröber 1936: 272, Fig 132); setulae on frons indistinct and confined to outermost lateral margins of frons (Fig. 131); ♀ theca semi-circular, with an elongated field of dense black setae, the anterior and posterior margins of which are almost parallel ..... ***P. caenostylata* Kröber, 1936**
- Maximum length of apical aristomere less than twice maximum length of projection of basal aristomere (Fig 149); setulae on frons more widely distributed, usually not only confined to outermost lateral margins of frons (Fig. 147); ♀ theca narrow, triangular, with rounded central field of dense black setae (Fig. 150) ..... ***P. pubescens* Brunetti, 1925**
  
- 5. Tibiae lacking dorsal lines of black setulae; scutum orange-brown, with three black stripes; ♀ unknown [based on the original description only]..... ***P. alineae* (Camras, 2001)**
- Tibiae with distinct lines of black setulae (e.g. Fig. 140); scutum completely black centrally ..... **6**
  
- 6. Basal aristomere projection shorter than apical aristomere (Fig. 137); setulae on vertex denser and therefore surface of vertex appears very roughened. Anterior part of vertex with a distinct area bare of setulae; setulae on vertex shorter, forming a level-topped pile in lateral view, the longest setulae on vertex being shorter than scape (Fig. 136); ♀ theca with crescentic apical field of long, blunt black setae, the longitudinal height of the field being distinctly greater than width (Fig. 139)..... ***P. goergeni* spec. nov.**
- Basal aristomere projection about same length as apical aristomere (Fig. 145); anterior part of vertex which lacks setulae indistinct and much smaller, and with a distinct depression (Fig. 143); setulae on vertex less dense and therefore surface of vertex appears less roughened (Fig. 143); setulae on vertex longer, becoming taller at rear in lateral view, the longest setulae on vertex about as long as scape; ♀ theca with a much broader field of black setae (Fig. 146) ..... ***P. nigrita* (Camras, 1962)**

***P. alineae* (Camras, 2001)**

*Pseudophysocephala alineae* Camras 2001

No material of this species has been seen by us. Only the male holotype is known, from Tanzania (Usambara Mountains, Amani) at 1000m.

***P. barbata* (Camras, 2001)**

(Figs 126–130)

*Pseudophysocephala barbata* Camras 2001

**Material.** SOUTH AFRICA: 1♂, 10.–22.xii.1930, Cape Province, Somerset East, paratype of *P. barbata*, det. as *P. constricta* by Kröber 1938, leg. R. E. Turner, coll. NHML [NHMUK010922128]; ZIMBABWE: 2♂♂, 28.x.1965, n Vumba [= Bvumba] [-19.093432 32.740631], paratype of *P. barbata*, leg. D. Cookson, coll. FMNH.

*Physocephala barbata* looks like *P. hirta* but with shorter setulae. Only the female holotype of *P. hirta* is known whilst only males are known of *P. barbata*, leading to the suspicion that they may be conspecific. It would be useful to find the opposite sex of one or other of these species to exclude the possibility of sexual dimorphism such as that observed in other species of the *pubescens* group.

***P. caenostylata* Kröber, 1936**

(Figs 131–133)

*Physocephala caenostylatus* Kröber 1936

**Primary type material examined.** ♀ holotype of *Physocephala caenostylatus* Kröber, 1936: (1) “*Ph. Type* ♂ / *caenostylus* [sic]”; (2) “Musée du Congo / Kibali-Ituri : Kilo / V-1930 / G. du Soleil”; (3) “R. DÉT / U / 2992”; (4) “*Physocephala* ♂ / *caenostylus* [sic] / Krb / det. Kröber 1935”; (5) “Typus”; (6) “RMCA ENT / 000012178”; coll. MRAC.

**Additional material.** KENYA: 1♀, 7.x.2013, S. Masai Reserve, des. as syntype of *P. pubescens*, leg. T. J. Anderson, coll. NHML [NHMUK010922163]; TOGO: 1♂, vi.2008, Kloto, forest area [6°57'31.66"N 0°34'29.75"E], leg. G. Goergen, coll. IITA.

Whilst identification of female *P. caenostylata* is straightforward males are very difficult. We are not convinced that all specimens can be safely distinguished from those of *P. pubescens*.

***P. goergeni* spec. nov.**

(Figs 134–142)

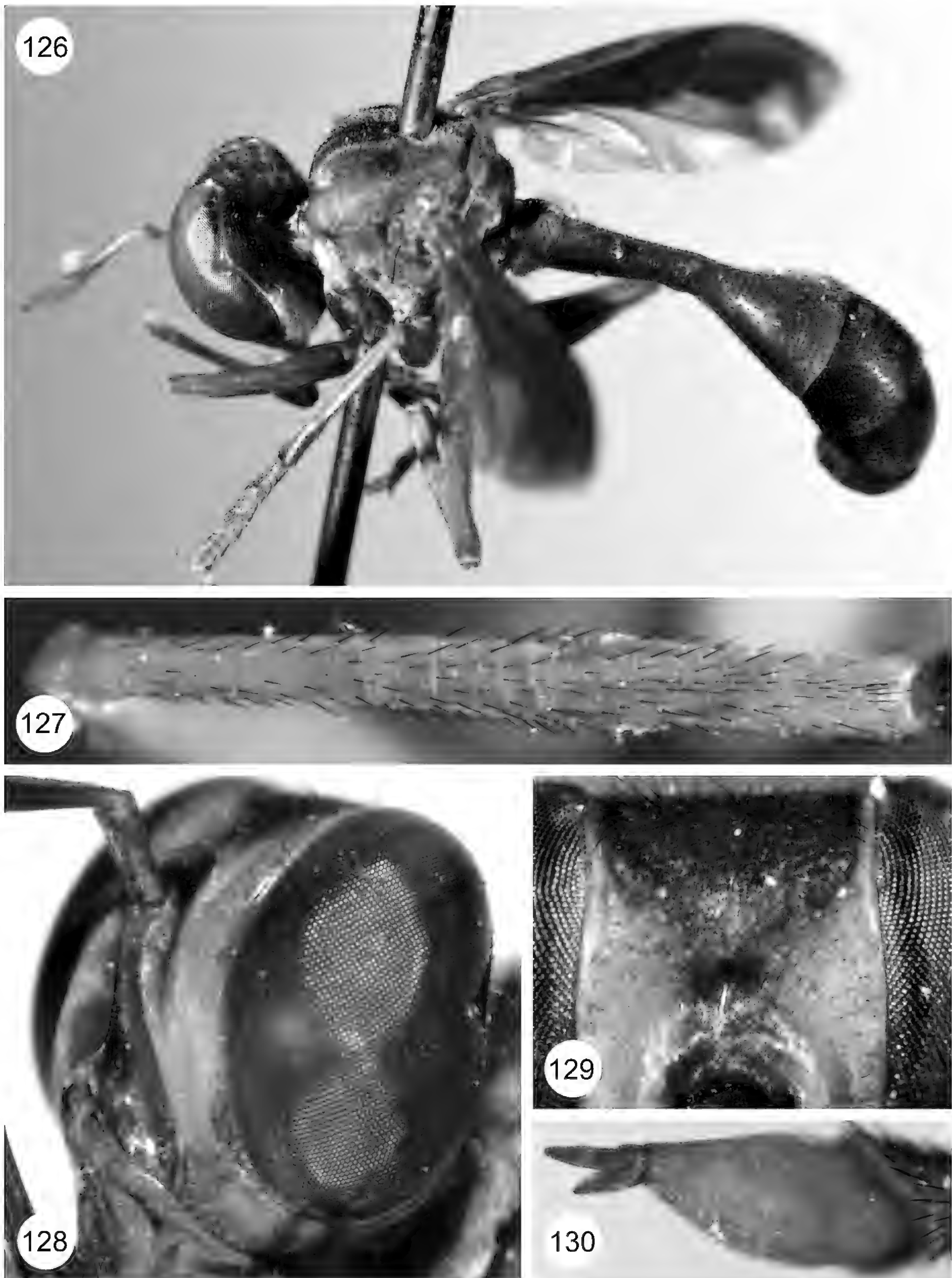
urn:lsid:zoobank.org:act:A4F67D5A-00A2-451D-8B10-59F1CA272EC0

**Holotype** ♀. (1) “Togo / Kloto / forest area / Feb. 2018 / Col.: G. Goergen”; (2) “Holotypus / *Physocephala goergeni* / spec. nov. ♀ / det. Stuke 2019”. Holotype is deposited in ZMHB. The specimen is pinned and in very good condition.

**Description of holotype (female)**

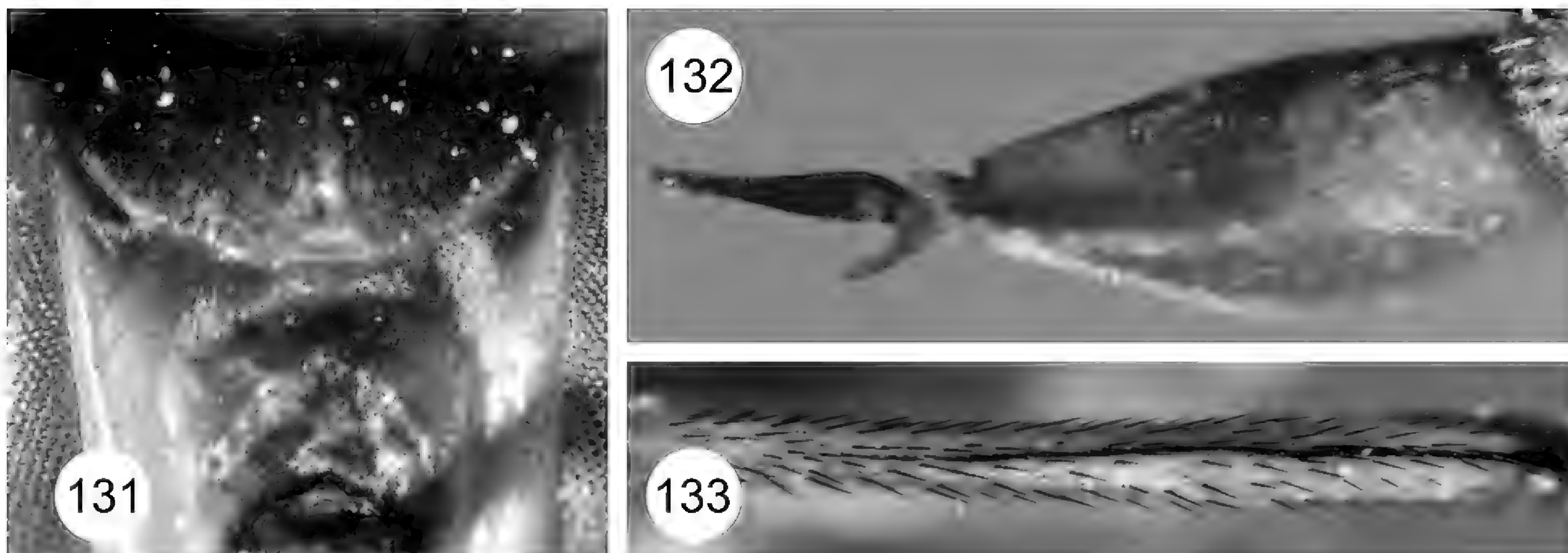
Length 10.8 mm; Wing-length 7.0 mm; Head-height 2.8 mm.





**Figs 126–130.** *Physocephala barbata* (Camras, 2001) (♂, paratype n Vumba). **126.** Habitus, lateral view; **127.** Middle tibia, dorsal view; **128.** Face, anterolateral view; **129.** Frons, dorsal view; **130.** Arista, lateral view.





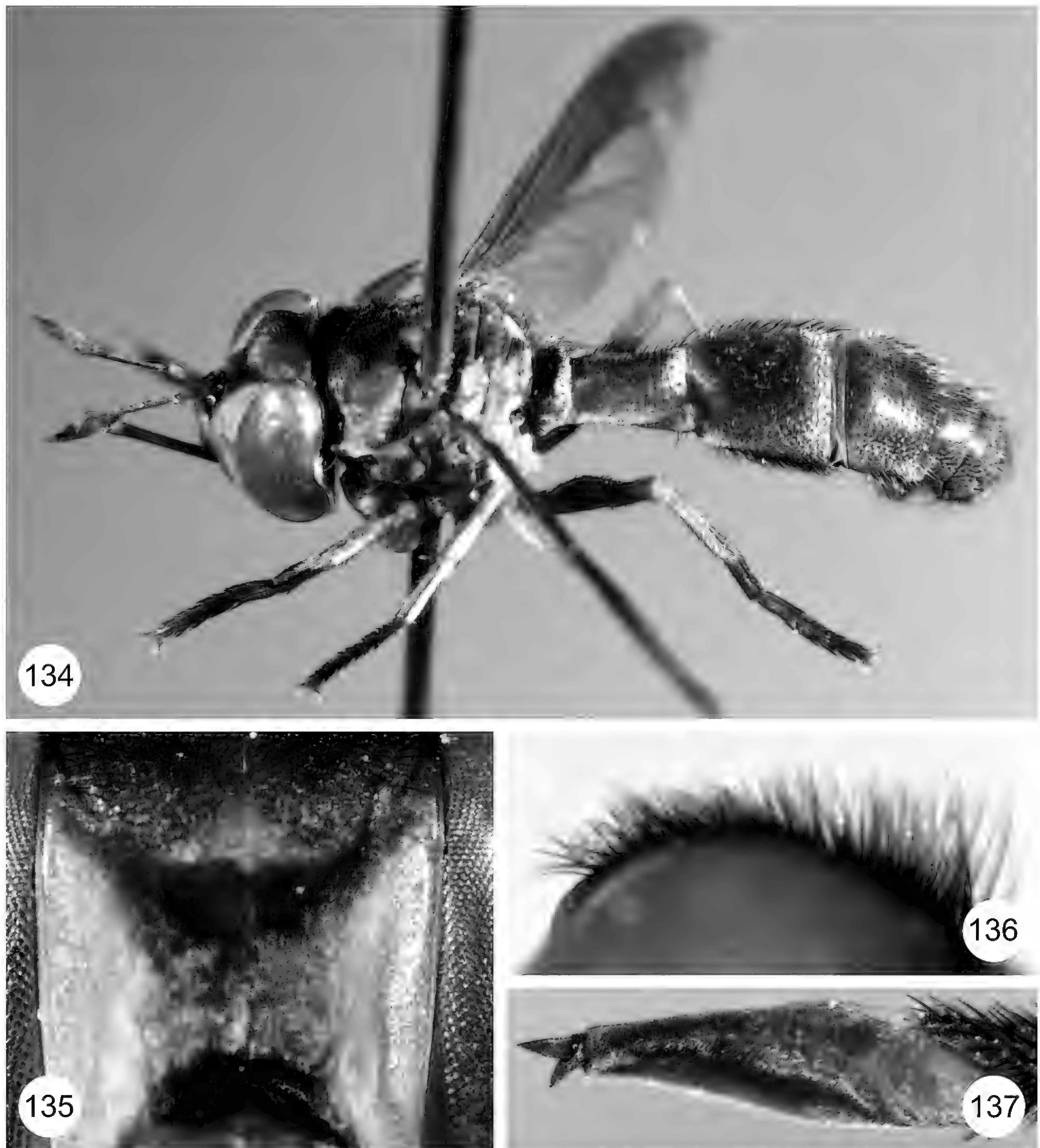
**Figs 131–133.** *Physocephala caenostylata* Kröber, 1936 (♂, Kloto). **131.** Frons, dorsal view; **132.** Arista, lateral view; **133.** Middle tibia, dorsal view.

**Head.** Antenna orange-brown, pedicel and tip of first flagellomere blackish-brown. Arista stylus-like, with 2 aristomeres situated at tip of first flagellomere (Fig. 137). Basal aristomere with projection about as long as apical aristomere. Scape about four times longer than maximum width, apically and ventrally with setae. Pedicel about six times longer than maximum width, apically and most of dorsal surface covered with black setulae. Pedicel lacking any ridge at base, expanded towards apex. First flagellomere long and conical, about three times as long as high, pointed, ventrally with indistinct membranous area. Lunule between base of antennae and ptilinal suture distinct, slightly longer than width of scape. Eye brown, lacking ommatrichia, facets all of about the same size. Posterior margin of eye with distinct shining indentation. Gena-height / eye-height (measurements taken from head in lateral view) = 0.1. No ocellar tubercle, no ocelli and no ocellar triangle evident. Frons (Fig. 135) longer than broad, slightly concave, not projecting above eyes posteriorly, lacking any setulae. Anterior margin of frons slightly concave. Frons yellow with broad brown midstripe. No frontofacial spot. Frons indistinctly dusted all over. Vertex as broad as frons, separated from latter by laterally distinct and medially indistinct ridge. Dense cover of black setulae on vertex forming a more or less level-topped pile in lateral view (Fig. 136). Vertex apically with triangular field which lacks setulae or any distinct depression. Face yellow with central brown to blackish spot. Facial grooves with indistinct dusting, narrowly dusted along eye margin. Gena yellow, generally lacking setae, although with several setae below postcranium. Distinct facial grooves reaching mouth edge, facial carina reaching from base of antennae to a distinctly broadened and outstanding frontoclypeal tubercle. Ptilinal suture stretching on either side well beneath antennal bases. Oral cavity tapers dorsally. Postcranium not obviously invaginated, black dorsally and yellow ventrally.

Whole postcranium slightly dusted, with no obviously denser dusting adjacent to posterior margin of eye. Occiput and postgena covered with black setulae. Postgena not widened and not delimited from occiput. Bottom portion of postcranium distinctly separated-off and not setulose. Proboscis reddish-brown basally and black apically, labellum blackish-brown. Frontoclypeal membrane long, light orange-brown and hardly delimited from orange-brown clypeus. Palps absent. Labium longer than head-length in lateral view, thickened basally, anterior section completely fused into a tube. Labrum as long as labium but very narrow. Labellum short, completely divided, hardly broader than adjacent haustellum, and covered with very short setulae.

**Thorax** mainly black, with pleura black to brown. Postpronotum orange-brown. Thorax evenly grey-dusted all over, lacking any distinctly denser dusting or shining areas. Presternum distinct, broad. Basisternum broad, not narrowed ventrally to a point, lacking setae or setulae. Proepisternum also lacking setae or setulae. Scutum covered with black setae. Notopleuron and postalarcallus with several stronger setae. Postalarcallus lacking any curved setulae beneath the black setae. Katepisternum with 10–15 setae posterodorsally, 1–2 setae medially, and no setae ventrally. Metakatepisternum, anepisternum and anepimeron lacking setae or setulae. Mediotergite convex, covered with strong black setae which can be as long as maximum diameter of hind femur. Subscutellum inconspicuous. Scutellum densely covered with black setae and with 3 outstanding larger setae on posterior margin. Wing as Fig. 142: Fore-margin of wing tinged brown, with brownish membrane between costa and media, brown basal-medial cell and slightly brownish hind-margin of discal-medial cell. Hyaline membrane between media and vena spuria in cell  $r_{4+5}$ . Veins brown to black. Wing completely covered with microtrichia. Radial-medial crossvein short but complete. Basal-me-



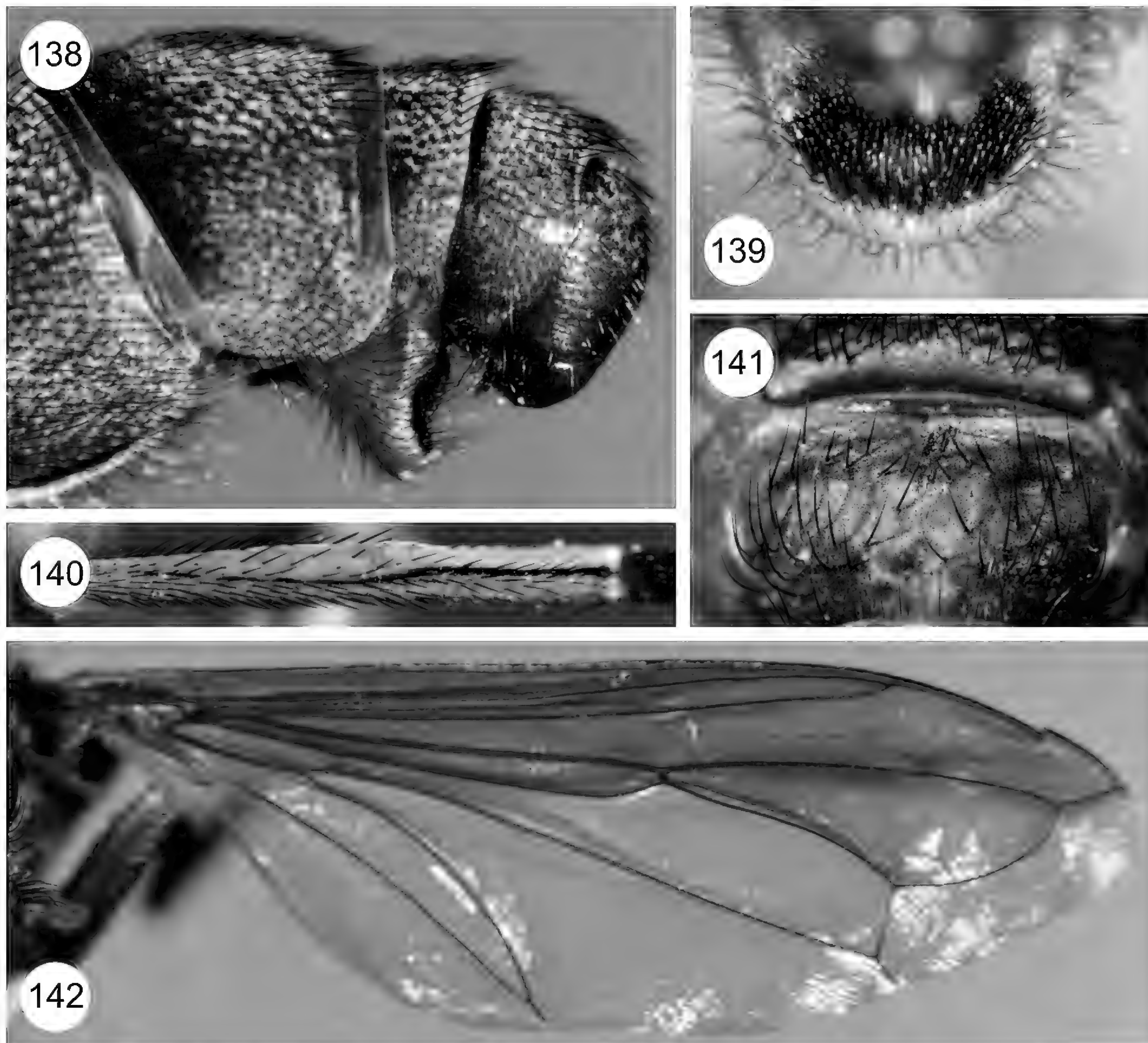


**Figs 134–137.** *Physocephala goergeni* spec. nov. (♀, holotype). **134.** Habitus, lateral view; **135.** Frons, dorsal view; **136.** Level-topped pile of setulae on vertex, lateral view; **137.** Arista, lateral view.

dial-cubital crossvein incomplete. Radius  $R_1$  and  $R_{2+3}$  terminate close together in costa, well beyond end of subcosta. Radius  $R_{4+5}$  with shallow, even curve in distal section directed towards fore-edge of wing. Cell  $r_{4+5}$  pedunculate, vein  $R_{4+5}+M_1$  well distinctly longer than radial-medial crossvein. Cubital cell cup elongated, lon-

ger than vein  $A_1+CuA_2$ , and pointed distally (i.e. cubitus  $CuA_2$  and anal vein  $A_1$  meet at an acute angle). Cubital veins  $CuA_1$  and Basal-medial-cubital crossvein separated. Upper and lower calypters yellowish-white to brown, upper calypter with black setulae on margin. Alula broad (distinctly broader than long), lacking setulae on posteri-





**Figs 138–142.** *Physocephala goergeni* spec. nov. (♀, holotype). **138.** ♀ theca, lateral view; **139.** ♀ theca, posterior view; **140.** Middle tibia, dorsal view; **141.** Mediotergite, posterior view; **142.** Wing, dorsal view.

or margin. Venae spuriae pronounced in cell  $r_{4+5}$ , cubital cells cup and cua1, and discal-medial cell. Haltere white, with light brown base. Knob of haltere with black setulae. Legs orange with black to dark brown tarsi. Legs with inconspicuous silver dusting, coxae densely silver-dusted. Posterior surfaces of fore and middle tibiae with obvious silver-dusted fields distally. Legs generally with short, adpressed black setulae. Base of fore and middle femora lacking denser black setulae basally. Areas with dense black to brown setulae anteroventrally on tip of fore tibia, and ventrally and posteriorly on tip of hind tibia. Middle femur lacking a distinct row of regularly arranged setulae. Hind femur ventrally with several long thin setulae. No preapical setae dorsally on tibiae. No setae ventral-

ly on tibiae but all tibiae dorsally with distinct line of densely-arranged small black setulae (Fig. 140). Femora ventrally lacking rows of short black setae, but with indistinct lines of setulae. Coxae with several setae but none outstandingly long. Hind femur slightly thickened in basal half. Each metatarsus with 1–2 stronger seta ventrally on base. Pulvilli yellowish-white. Claws brown, with broad black tips. Empodium light brown, about as long as pulvilli.

**Abdomen** dark brown to black, with theca and lateral margins of tergites 2–3 orange-brown. Abdomen with dense black setulae all over, those on tergite 2 less dense and obviously longer. Abdomen entirely somewhat silver, brown or golden-dusted, more strongly so at hind



margins of tergites 1–3. Tergite 8 shining. Tergites 1–3 fused and hardly distinguishable from each other. Maximum width of abdomen at segment 3. Sternites cannot be seen due the ventrally overlapping tergites. Tergite 5 and sternite 5 not completely fused laterally. Shape of theca as Figs 138 & 139. Anterior surface of the theca with long black setulae. Posterior surface apically with crescentric field of long, blunt, close-set black spicules which stand very close together, not arranged in rows.

### Diagnosis

*Physocephala goergeni* is easily identified as member of the *Physocephala pubescens* species-group by the long setae on the mediotergite (Fig. 141). Within this group it belongs among those species which lack any setulae on the frons. The shape of the field of thick black setae on the theca distinguishes ♀ *P. goergeni* immediately from *P. nigrita* (Fig. 139 vs. Fig. 146). Additional important characters include the level-topped pile of setulae on the vertex (Fig. 136) and the shorter basal aristomere (cf Fig. 137 vs. Fig. 145).

### Etymology

This species is dedicated to Georg Goergen (Ibadan, Nigeria) who collected the holotype, and who appears to be the first entomologist to collect Conopidae in Benin and Togo.

### Distribution

To date only the locus typicus in Togo is known. The sampling site is situated at 6°57'31.66"N 0°34'29.75"E.

### *P. hirta* (Kröber, 1939)

*Pseudophysocephala hirta* Kröber 1939

**Primary type material examined.** ♀ holotype of *Pseudophysocephala hirta* Kröber 1939: (1) "Holo-/type"; (2) "Type"; (3) "E. Cape Prov. / Katberg. / 1.–10.ii.1933."; (4) "S. Africa. / R. E. Turner. / Brit. Mus. / 1933-139."; (5) "*Pseudophysocephala* / *hirta* Kröber / examined & det. / O. Kröber, 1938."; coll. NHML

See comment under *Physocephala barbata* (Camras, 2001), above.

### *P. nigrita* (Camras, 1962)

(Figs 143–146)

*Pseudophysocephala nigrita* Camras 1962

= *Pseudophysocephala brevivertex* Camras 2001 (syn. nov.)

**Material.** CAMEROON: 1♀, 17.–19.viii.2003, Northwest Reg., Mezam, Bafut village [06°05.026'N 10°07.442'E], 1060 m, leg. A. H. Kirk-Spriggs, coll. BMSA; KENYA: 2♀, 4.–11.xii.1999, Western Province, Kakamega Forest, Malaise trap [0°14.13'N 34°51.87'E],

leg. R. Copeland, coll. NMKE; 1♀, 16.–23.viii.2000, ditto; TOGO: 1♂, ii.2017, Kloto, forest area [6°57'31.66"N 0°34'29.75"E], leg. G. Goergen, coll. IITA; 1♀, viii.2015, ditto; UGANDA: 1♂, vii.–viii.1946, Bwamba, leg. van Someren, coll. NHML [NHMUK010922185]; 1♀, vii.–viii.1946, ditto [NHMUK010922187]; 1♂, 16.xii.1934, Kampala, flying against bees, leg. T. W. Chorley, coll. NHML [NHMUK010922191]; 1♂, 18.ii.1966, Lake Nabugabo, det. as *P. nigrita* by Camras 2000, leg. D. J. Greathead, coll. NHML [NHMUK010922156].

The main character given to distinguish *P. brevivertex* in the original description of Camras (2001) was a "short vertex". This character is difficult to assess, however, because the vertex may be tightly curved and of variable shape in the material to hand. Apically the vertex has an area which is not covered with setulae and which may have a depression, but the shape, size and extent of any depression can vary considerably, giving a different impression of the vertex shape. There is no other character available to distinguish *P. brevivertex* from *P. nigrita*, and therefore *Physocephala* [*Pseudophysocephala*] *brevivertex* Camras, 2001 is herewith placed as a junior synonym of *Physocephala* [*Pseudophysocephala*] *nigrita* Camras, 1962 (syn. nov.).

### *P. pubescens* Brunetti, 1925

*Physocephala pubescens* Brunetti 1925

= *Physocephala curta* Kröber 1936

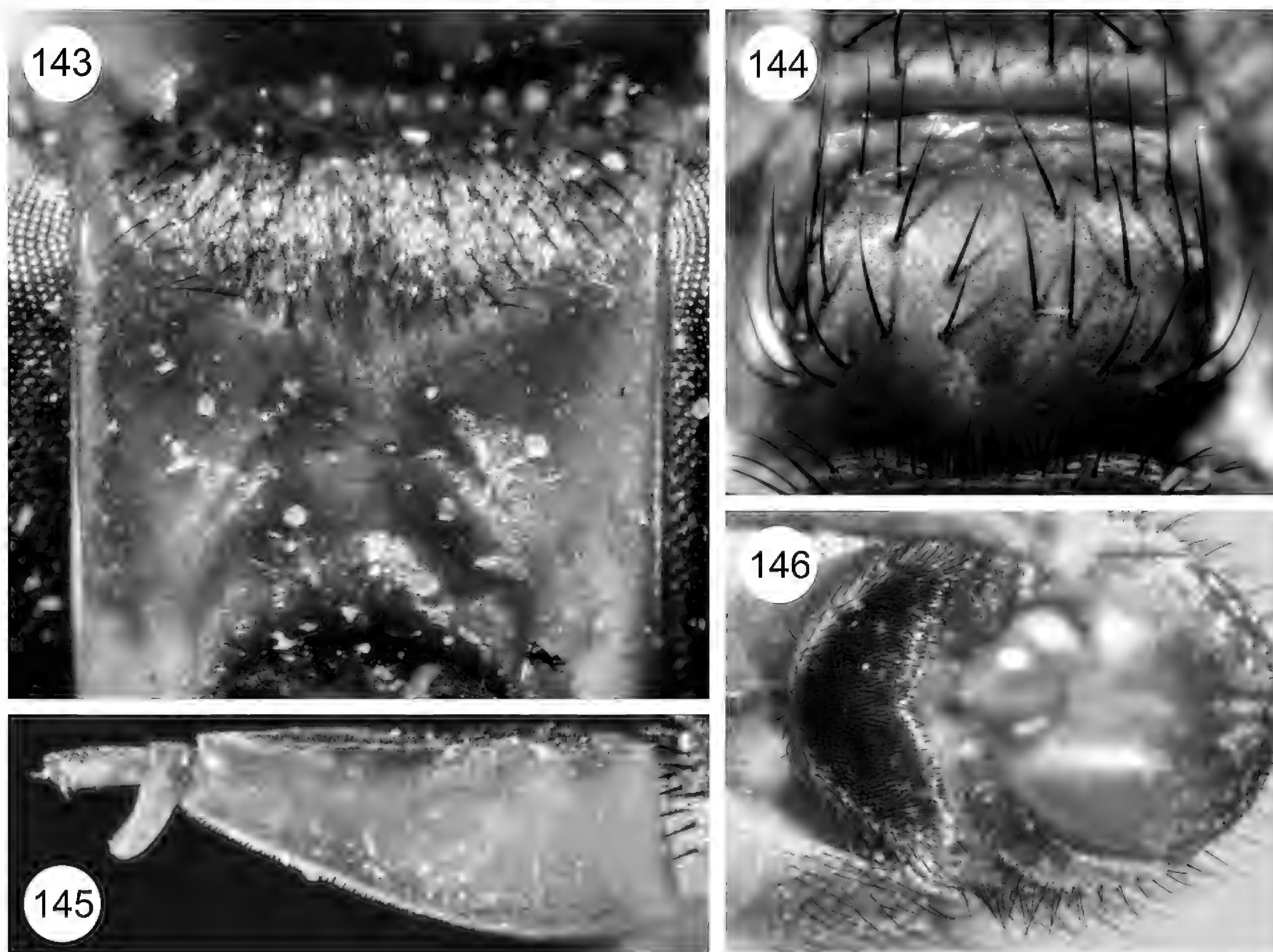
(Figs 147–151)

**Primary type material examined.** ♂ lectotype of *Physocephala pubescens* Brunetti 1925 herewith designated: (1) "Syn - / type"; (2) "23.9.16 / Limbe / Nyasaland. / 4000' (R. C. W.) / R. b. Wood / 684."; (3) "*Physo. / pubescens* / Brun Type ♂ / Det. E. Brunetti 1924"; (4) "Lectotypus / *Physocephala* / *pubescens* ♂ / Brunetti, 1925 / des. Stuke 2019"; NHML.

♀ lectotype of *Physocephala curta* Kröber, 1936 herewith designated: (1) "Type / *Ph. curta* ♀"; (2) "Musée du Congo / Elisabethville / 1927 / Dr. M. Bequaert"; (3) "*Physocephala* / *curta* Krb. / det. Kröber 1935"; (4) "R. DÉT / L / 2992"; (5) "Type"; (6) "RMCA ENT / 000012182"; coll. MRAC.

**Additional material.** DEMOCRATIC REPUBLIC OF CONGO: 1♂, no date, Elisabethville [Lubumbashi] [-11.664232 27.482626], det. as *P. pubescens* by Camras 1962, leg. M. Bequaert, coll. FMNH; KENYA: 1♀, ii.1932, Kijabe, det. as *P. pubescens* by Camras 1962, leg. van Someren, coll. NHML [NHMUK010922169]; 1♀, 20.iii.1949, Nairobi, det. as *P. pubescens* by Camras 1962, leg. G. Salt, coll. NHML [NHMUK010922168]; 1♂, 9.iv.1949, Nairobi, det. as *P. pubescens* by Camras, 2000, leg. G. Salt, coll. NHML [NHMUK010922188]; 1♀, 3.vii.1994, Nairobi, leg. R. Copeland, coll. NMKE;





**Figs 143–146.** *Physocephala nigrita* Camras (1962). **143.** Frons, dorsal view (♂, Bwamba); **144.** Mediotergite, posterior view (♀, Bafut village); **145.** Arista, lateral view (♀, Bafut village); **146.** ♀ theca, ventral view; (♀, Bafut village).

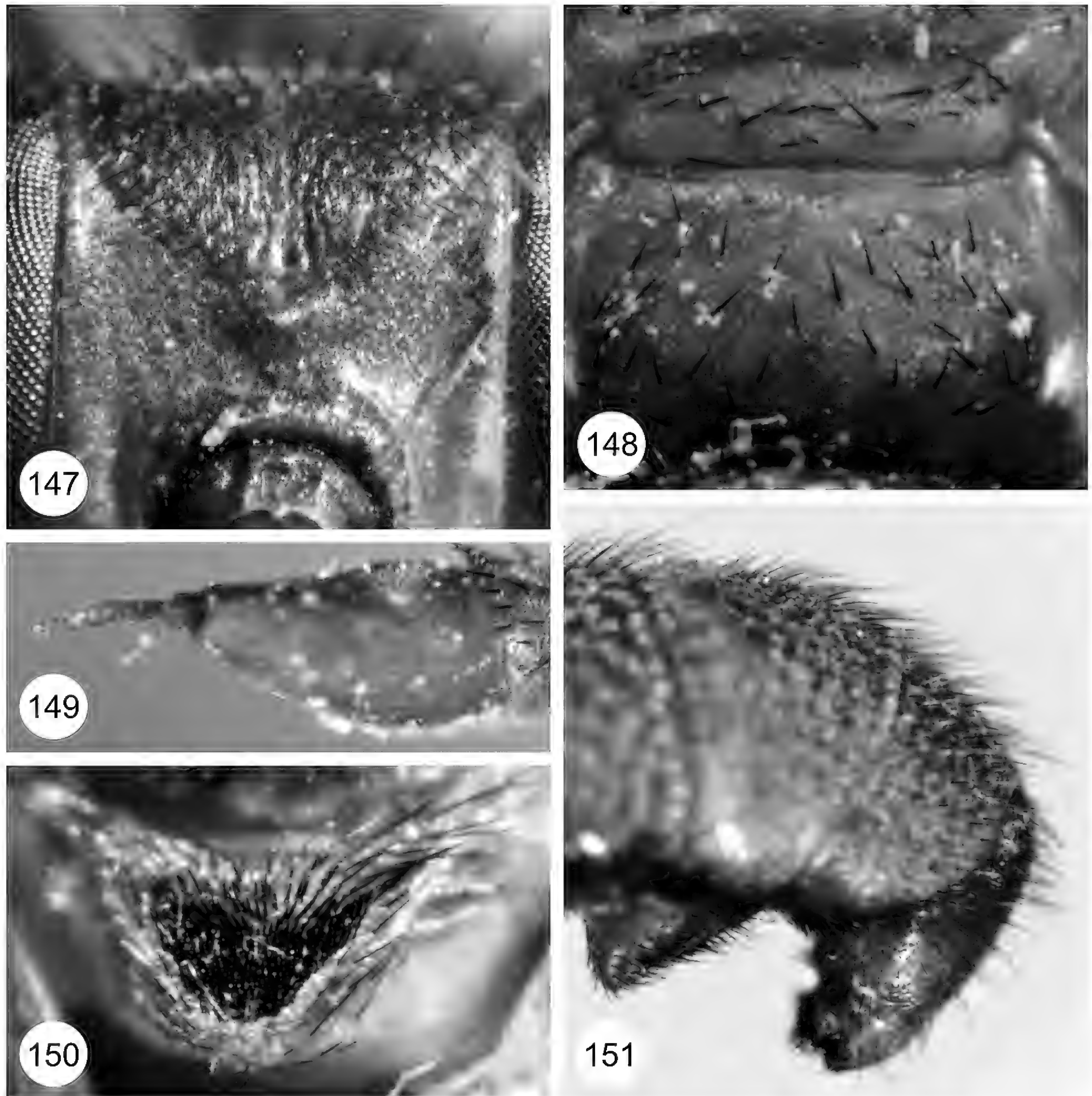
1♂, 12.viii.1966, Nairobi, 5400 ft, det. as *P. pubescens* by Smith, 1967, leg. G. R. C. van Someren, coll. NHML [NHMUK010922186]; 1♂, 2.i.1997, Nairobi, Kebete, 1800 m, leg. T. Romig, coll. PMHA; MALAWI: 1♂, 17.iii.1913, Nyasaland, Mlanje [= Mulanje], des. as syntype of *P. pubescens*, leg. S. A. Neave, coll. NHML [NHMUK010922166]; 1♂, 6.xi.1912, Nyasaland, Mt. Mlanje [= Mulanje Massif], des. as syntype of *P. pubescens*, leg. S. A. Neave, coll. NHML [NHMUK010922165]; 1 specimen, 1.x.1913, Nyasaland, Mt. Mlanje [= Mulanje Massif], des. as syntype of *P. pubescens*, leg. S. A. Neave, coll. NHML [NHMUK010922164]; UNKNOWN LOCATION: 1♀, iv.1941, “Mtowambo”, det. as *P. pubescens* by Camras 1962, leg., coll. FMNH; 1♀, viii.1943, [characters illegible], det. as *P. pubescens* by Camras 1962, leg. H. J. A. Turner, coll. NHML [NHMUK010922167].

The material held under ‘*Physocephala pubescens*’ at the NHML includes four syntypes of *P. pubescens* and two syntypes of *P. curta*. The former comprises a mixture of *P. pubescens* and *P. caenostylata* Kröber, 1936. It is

therefore necessary to designate a lectotype for *P. pubescens* and we herewith select a male syntype from Limbe which agrees with the species concept as here defined in order to prevent any change in the past usage of this name.

Stuke (2017a) incorrectly stated that Smith (1980) had synonymized *P. curta* with *P. pubescens* when in fact this was done by Camras (1962). Re-examination of the two *P. curta* syntypes held at NHML concluded that these also comprise multiple species. The female syntype from Elisabethville is identical with *P. pubescens*, and in order to prevent further confusion we herewith designate this specimen as the lectotype of *P. curta*. The second syntype belongs to *P. microvena* Brunetti, 1925 and bears the labels: (1) “Paratype / *Ph. curta* ♀”; (2) “Musée du Congo / Ituri: Blukwa / 10 - XI - 1928 / A. Collart”; (3) “Cotype”; (4) “*Physocephala* ♀ / *curta* Krb. / det. Kröber 1935”; (5) “R. DÉT / M / 2992”; coll. MRAC. This specimen has, unusually, a distinctly developed radial-medial crossvein and could therefore easily be confused with other species.





**Figs 147–151.** *Physocephala pubescens* Brunetti 1925. **147.** Frons, dorsal view (♂, Nairobi); **148.** Mediotergite, posterior view (♂, Nairobi); **149.** Arista, lateral view (♂, Nairobi); **150.** ♀ theca, posteroventral view (♀, Nairobi); **151.** ♀ theca, lateral view (♀, Nairobi).

#### *Physocephala vittata* species-group

This group contains only *P. vittata*, which Camras (2001) included (as *P. maculigera* Kröber, 1915) in his *Physocephala maculipes* species-group. The *vittata* group is very similar to the *Physocephala antiqua* species-group due to its typical *Physocephala* habitus (as described in Key 1) and short arista. Both species-groups can be distinguished by the characters given in Key 1, however. A

second member of this species-group – *P. schmideggeri* Stuke, 2017 – has been recorded from the Arabian Peninsula and could also potentially occur in the Afrotropical Region. These species can be distinguished using Stuke (2017b). *Physocephala vittata* is primarily a widespread Palearctic species which reaches as far as Mongolia and China, as well as extending into the Afrotropical Region.



***P. vittata* (Fabricius, 1794)***Conops vittata* Fabricius 1794

**Material.** ERITREA: 1♀, 28.ix.1957, Taramna, det. as *P. maculigera* by Camras 2000, leg. D. J. Greathead, coll. NHML [NHMUK010922106]; ETHIOPIA: 1♀, 3.iv.2016, SNNPS State, Arba-Minch, Dorze [06°10'N 37°35'E], 2340 m, leg. J. Halada, coll. CULSP.

***Physocephala*, species not recognised*****P. nigerrima* Kröber, 1915***Physocephala nigerrima* Kröber 1915

*Physocephala nigerrima* was only known from the female holotype, which is probably lost (Stuke 2017a). Camras (2001) placed this species in his *Physocephala maculipes* species-group although this interpretation does not fit with the original description. Kröber described the arista as being pointed and slender, and the lateral projection also, with both being of almost equal length (“Griffel spitz und zart, Seitenfortsatz ebenfalls, beide fast gleich lang”) and the antenna as long, very slender and black, with the first flagellomere rusty brown and the scape about three times as long as its width at the base and slightly widened towards the tip (“Fühler lang und sehr schlank, schwarz, drittes Glied rostbraun. Erstes Glied etwa dreimal so lang als unten breit, oben wenig verbreitert.”). This species cannot readily be placed and in the absence of any available material we therefore propose to classify *Physocephala nigerrima* Kröber, 1915 as an unrecognised species (**status rev.: nomen dubium**) until such time as new material appears.

**Acknowledgements.** We would like to thank all of the colleagues who have supported this work with their generous help: Miroslav Barták (Czech Republic, Prague), Eliana Buenaventura (Germany, Berlin), Pasquale Ciliberti (Netherlands, Leiden), Robert Copeland (Kenya, Nairobi), Wouter Dekoninck (Belgium, Brussels), Hans-Joachim Flügel (Germany, Knüllwald), Amnon Freidberg (Israel, Tel Aviv), Georg Goergen (Benin, Calavi), Martin Hauser (USA, Sacramento), Christian F. Kassebeer (Germany, Damlos), Ashley H. Kirk-Spriggs (formerly South Africa, Bloemfontein, now UK, London), Tom Kirschey (Berlin), Maurizio Mei (Italy, Rome), Ximo Mengual (Germany, Bonn), Frank Menzel (Germany, Müncheberg), Crystal Maier (USA, Chicago), Marc de Meyer (Belgium, Tervuren), Wolfgang Schacht (Germany, †), Karla Schneider (Germany, Halle), Peter Sehnal (Austria, Vienna), Axel Ssymank (Germany, Bonn), Nigel Wyatt (UK, London) and Joachim Ziegler (Germany, Berlin), all of whom provided material either from their private collections or from collections under their care. Martin Hauser in particular sorted through a huge amount of Conopidae from Malaise trap samples and made it available for our research. While visiting collections to look at Afrotropical Conopidae we received generous help from Nigel Wyatt (UK, London), Erica McAlister (UK, London), Sven Marotzke (Germany, Berlin), Jenny Pohl (Germany, Berlin), Joachim Ziegler (Germany, Berlin), Eliana Buenaventura (Germany, Berlin),

Marc de Meyer (Belgium, Tervuren), Stéphane Hanot (Belgium, Tervuren), Wouter Dekoninck (Belgium, Brussels) and Frank Menzel (Germany, Müncheberg). With great skill, Nygel Wyatt decoded illegible writing and characters on the labels of many historical specimens.

**REFERENCES**

- Borkent A (2018) The state of Phylogenetic Analysis: Narrow Visions and Simple Answers – Examples from the Diptera (Flies). *Zootaxa* 4374: 107–143
- Camras S (1957) On some Conopidae (Dipt.) from Flores and Sumba. *Wissenschaftliche Ergebnisse der Sumba-Expedition des Museums für Völkerkunde und des Naturhistorischen Museums in Basel, 1949. Verhandlungen der naturforschenden Gesellschaft in Basel* 68: 160–164
- Camras S (1962a) The Conopidae of Madagascar (Diptera). *Mémoires de l'Institut Scientifique de Madagascar, serie E* 13: 179–187
- Camras S (1962b) Records and descriptions of African Conopidae (Diptera). *Revue de Zoologie et de Botanique Africaines* 66: 203–242
- Camras S (1965) Family Conopidae. Pp. 625–632 in: Stone A, Sabrosky CW, Wirth WW, Foote RH & Coulson JR (eds) *A catalog of the Diptera in America North of Mexico*. Smithsonian Institution Press, Washington
- Camras S (2001) Additional information on Afrotropical Conopidae. *Entomologist's Monthly Magazine* 137: 179–210
- Cumming JM, Wood DM (2009) Adult Morphology and Terminology. Pp. 9–50 in: Brown BV, Borkent A, Cumming JM, Wood DM, Woodley NE & Zumbado MA (eds): *Manual of Central American Diptera*. Volume 1: 1–714. NRC Research Press, Ottawa.
- GBIF (2019) Free and open access to biodiversity data. <https://www.gbif.org> [last access 18.11.2019]
- Gibson JF, Skevington JH (2013) Phylogeny and taxonomic revision of all genera of Conopidae (Diptera) based on morphological data. *Zoological Journal of the Linnean Society* 167: 43–81
- Kotrba M (2000) 1.3 Morphology and terminology of the female postabdomen. Pp. 75–84 in: Papp L & Darvas B (eds): *Contributions to a Manual of Palearctic Diptera*. Volume 1. General and Applied Dipterology. Science Herald, Budapest.
- Kröber O (1915) Die afrikanischen Arten der Gattung *Physocephala* Schin. *Archiv für Naturgeschichte, Abteilung A* 80(11): 81–99
- Kröber O (1939) Beiträge zur Kenntnis der Conopiden. I. *Annals and Magazine of Natural History* 11(4): 362–395
- Smith KGV (1980) 39. Family Conopidae. Pp. 511–517 in: Crosskey RW (ed.): *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London.
- Smith KGV, Cunningham-van Someren GR (1970) The identity of *Physocephala bimarginipennis* Karsch (Diptera, Conopidae) with notes on the immature stages and biology. *Journal of Natural History* 4: 439–446
- Smith KGV, Peterson BV (1987) 54. Conopidae. Pp. 749–756 in: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR & Wood DM (eds): *Manual of Nearctic Diptera*. Volume 2. Monograph of the Research Branch Agriculture Canada 11: vi + 658 pp; Ottawa.
- Stuke J-H (2015a) New Conopid records from the Afrotropical Region (Diptera). Part 1: *Paramyopa* Kröber, *Pseudoconops* Camras, *Stylogaster* Macquart, *Thecophora* Rondani and *Zodion* Latreille. *Zootaxa* 3963: 101–159



- Stuke J-H (2015b) A contribution to the knowledge of *Physocephala antiqua* (Wiedemann) (Diptera: Conopidae). *Studia Dipterologica* (Müncheberg) 21: 209–220
- Stuke J-H (2016): Taxonomic notes on West Palaearctic Conopidae (Diptera). *Zootaxa* 4178: 521–534
- Stuke J-H (2017a): *World Catalogue of Insects*. Volume 15. Conopidae (Diptera). E. J. Brill, Leiden, Boston
- Stuke J-H (2017b): Order Diptera, family Conopidae. Description of a new species of *Physocephala* Schiner. *Arthropod Fauna of the UAE* 6: 613–620
- Stuke J-H (in press): New conopid records from the Afrotropical Region (Diptera). Part 2: Conopinae excluding Physocephalini. *Israel Journal of Entomology*



BHL



Blank Page Digitally Inserted



## Report \*\*

# A prelude to the Caucasus Barcode of Life Platform (CaBOL): Biodiversity Days in Georgia in 2018 and 2019

Jana Thormann<sup>1</sup>, Dirk Ahrens<sup>1</sup>, Cort Anderson<sup>2</sup>, Jonas J. Astrin<sup>1,\*</sup>, Levan Mumladze<sup>3</sup>, Björn Rulik<sup>1</sup>,  
 David Tarkhnishvili<sup>1</sup>, Marianne Espeland<sup>1</sup>, Matthias Geiger<sup>1</sup>, Nils Hein<sup>4</sup>, Giorgi Iankoshvili<sup>2</sup>,  
 Elisabeth Karalashvili<sup>2</sup>, Ximo Mengual<sup>1</sup>, Carsten Morkel<sup>5</sup>, Marco T. Neiber<sup>6</sup>, Ralph S. Peters<sup>1</sup>,  
 André Reimann<sup>7</sup>, Axel Ssymank<sup>8</sup>, Thomas Wesener<sup>1</sup>, Joachim Ziegler<sup>9</sup> & Bernhard Misof<sup>1,\*</sup>

<sup>1</sup>*Zoologisches Forschungsmuseum Alexander Koenig, Leibniz Institute for Animal Biodiversity, Center for Taxonomy and Evolutionary Research, Adenauerallee 160, D-53113 Bonn, Germany*

<sup>2</sup>*Center of Biodiversity Studies, Institute of Ecology, Ilia State University, Cholokashvili ave.3/5, GE-0169 Tbilisi, Georgia*

<sup>3</sup>*Institute of Zoology, Ilia State University, Cholokashvili ave.3/5, GE-0169 Tbilisi, Georgia*

<sup>4</sup>*School of Natural Sciences and Engineering Ilia State University, 3/5 Cholokashvili Ave, GE-Tbilisi 0162, Georgia*

<sup>5</sup>*Institute for Applied Entomology, Bartholomäusstrasse 24, D-37688 Beverungen*

<sup>6</sup>*Centrum für Naturkunde (CeNak) – Center of Natural History, Abteilung Biodiversität der Tiere, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany*

<sup>7</sup>*Senckenberg Naturhistorische Sammlungen Dresden, Museum für Tierkunde, Königsbrücker Landstraße 159, D-01109 Dresden, Germany*

<sup>8</sup>*Falkenweg 6, D-53343 Wachtberg*

<sup>9</sup>*Museum für Naturkunde, Invalidenstrasse 43, D-10115 Berlin, Germany*

\*Corresponding authors: Email: [j.astrin@leibniz-zfmk.de](mailto:j.astrin@leibniz-zfmk.de); [b.misof@leibniz-zfmk.de](mailto:b.misof@leibniz-zfmk.de)

**Abstract.** Here we report on collaborative expeditions run by ISU (Ilia State University, Tbilisi), ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn) and external taxonomists in Georgia in 2018 and 2019 as part of the renewed close cooperation between Germany and Caucasus countries aiming at the exploration of biodiversity in the Caucasus region. The 2018 and 2019 field work campaigns serve as a starting point for a larger cooperative venture, planned to start in 2020 – the Caucasus Barcode of Life Platform (CaBOL). To encourage participation by additional partners and to build an active expert network, we here describe the so-far collected material and collection methods, provide detailed information on collecting sites and the diversity of habitats and outline the goals of the planned CaBOL project. Building on experiences from the German Barcode of Life (GBOL) initiative, our goal is to increase expertise and capacity in the region for modern integrative taxonomy approaches.

**Keywords.** GBOL, GGBC, DNA barcoding, Kintrishi, Kazbegi.

## აბსტრაქტი

წინამდებარე ნაშრომში წარმოდგენილია სახელმწიფო უნივერსიტეტის (ISU), ალექსანდრ კოენიგის ზოოლოგიური კვლევითი მუზეუმი (ZFMK) და სხვა ტექსონომების მიწაწილობით საქართველოში ბიომრავალფეროვნების შესასწავლად 2018 და 2019 წლებში განხორციელებული ჯგუფური ექსპედიციების ანგარიში. ასევე გაგაცნობთ გერმანიასა და კავკასიის ქვეყნებს შორის მიმდინარე აქტიური თანამშრომლობას, რომელსაც მიზნად კავკასიის რეგიონის ბიომრავალფეროვნების ურყევედ მასშტაბური კვლევა. 2018 და 2019 წლის ექსპედიციები წარმოადგენს საასტრუქონომიული ჯგუფის მასშტაბური თანამშრომლობის რეგიონალური პროექტი – კავკასიის სიცოცხლის ბარკოდირება (CaBOL), რომელსაც დაწყებულია 2020 წლიდან დაგეგმილი დამატებითი პარტნიოების მოძიება და ჩართვისათვის ამ თანამშრომლობაში და შესაბამისად ბიომრავალფეროვნების ექსპერტების ქსელის გაფართოების ხელშეწყობისათვის, წარმოადგენდა ტალღას აღნიშნული ექსპედიციების პირველად შედეგების და CaBOL პროექტის მიზნებისა და გეგმების შესახებ. გერმანიის სიცოცხლის ბარკოდირების (GBOL) ინიციატივიდან მიღებული გამოცდილების გათვალისწინებით ჩვენი მიზანია რეგიონში გავზარდოთ ბიომრავალფეროვნების შესახებ ცოდნა და ინფრასტრუქტურული/ექსპერტული შესაძლებლობები თანამედროვე ტექსონომიური მიდგომების გათვალისწინებით.

## INTRODUCTION

The Caucasus Region is an area situated between the Black and the Caspian Sea, and is recognized as one of the global biodiversity hotspots (Mittermeier et al. 2004; Myers et al. 2000; Zazanashvili et al. 2004). Where Western Asia meets Eastern Europe, Georgia is bounded to the west by the Black Sea, to the north by Russia, to the south by Turkey and Armenia, and to the southeast by Azerbai-

jan. While making rapid strides towards modernization of its research and educational capacity, Georgia still lacks some key elements in both expertise and infrastructure. Targeted investment in science and education in Georgia is one of the major goals of our research collaboration, and perhaps the best way to develop and augment capacity for the essential biodiversity assessment *in situ*. It is most effective in close cooperation with an experienced partner. Germany and the Zoological Research Museum



Alexander Koenig, Bonn (ZFMK) are leaders in biodiversity research within Europe, for example, coordinating the German Barcode of Life (GBOL) initiative that has been successfully run for the last eight years and has delivered an operative DNA barcode reference library for German animals, plants and fungi (Geiger et al. 2016). Based on this Germany-focused biodiversity research, scientists from Georgia and Germany decided to launch a collaborative initiative to adapt the structure and strategy of the GBOL project to enable comprehensive biodiversity research in the species-rich Caucasus region. This paper documents the joint field work done so far, and gives an overview of the ongoing and future collaboration.

## PREVIOUS PROJECTS AND TRANSFER OF DNA BARCODING WORKFLOWS

Since 2012 ZFMK has led the GBOL project in which several German research institutions successfully worked together on a high-throughput sequencing pipeline to create an extensive DNA barcode library (Hebert et al. 2003a, 2003b) of the German fauna, flora and fungi in order to assess and access the national biodiversity (e.g., Raupach et al. 2014, Wesener et al. 2015, Astrin et al. 2016, Morinière et al. 2017, Rulik et al. 2017). Applying DNA barcodes for species identification and delimitation requires a database of reference sequences. In order to develop such a reference library, concerted efforts of taxonomists, biodiversity data specialists, and experts on molecular techniques are necessary. In 2017, the ZFMK made the first steps for a knowledge transfer from the GBOL project to Georgia, a country with a considerable need and potential for barcode-aided biodiversity assessment (Mumladze et al. 2019). In September 2017, a proposal for the development of a Georgian-German biodiversity center (GGBC) was granted by the German Federal Ministry of Education and Research (BMBF) (project's website: <https://ggbc.eu/>). The goal of the GGBC is to establish an infrastructure and to provide suitable training that allows the long-term development of a DNA barcode reference database for Georgia.

The operational infrastructure of the GBOL initiative is supposed to serve as a model, guiding the development of a comparable structure in Georgia. Such developments of the relevant infrastructures are planned to go hand in hand with taxonomic and methodological training of Georgian students, species identification by taxonomic experts, as well as molecular laboratory work. To this end, a lively exchange of students and researchers has already been established between ISU (Ilia State University, Tbilisi) and ZFMK.

## THE KINTRISHI PROJECT: MALAISE TRAP TRANSECT & BIODIVERSITY DAYS 2018

Within the framework of GGBC, the Kintrishi project was the first pilot project launched by the ISU-ZFMK collaborative team in April 2018. The project aimed to investigate the biodiversity in the Kintrishi Protected Areas and to start compiling a Georgian reference database of DNA barcodes for selected taxa. Created in 1959, the Kintrishi National Park is located in south-western Georgia (41°75' N, 42°03' E) and currently encompasses over 13,893 hectares (APA, 2019). Together with the adjacent Mtirala National Park, Kintrishi is the most humid area in the Caucasus region, with an annual precipitation of around 2500 mm (Neidze, 2003). It is a Plio-Pleistocene refugium featuring many relict and endemic animal and plant species (Kikvidze & Ohsawa 1999, Denk et al. 2001, Milne & Abbott 2002, Shatilova et al. 2011, Tarkhnishvili et al. 2011). The park ranges from 300 m up to 2,500 m a.s.l. and includes pristine mountain humid forests and subalpine/alpine habitats. Although the high level of biodiversity in Kintrishi was recognized early in the 20th century a validated catalog of animal and plant taxa in Kintrishi and surroundings is still lacking (Garsztecki 2017).

In April 2018, Björn Rulik and Ameli Kirse from the ZFMK spent two weeks in Georgia. Together with Levan Mumladze (ISU) and a group of Georgian students they set up Malaise traps along an elevational gradient in the Kintrishi gorge, from the lower reaches of the Kintrishi River (400 m a.s.l.) up to alpine meadows (2,500 m a.s.l.). Three trap replicates were placed at each of the six selected elevation levels (i.e., 18 traps in total) (Figs 1–3). The traps were emptied every two weeks by a team of Georgian students: Eka Arsenashvili, Giorgi Bakuradze, Giorgi Bananashvili, Giorgi Chikorashvili, Shota Japarashvili, Tinatin Chkhartishvili, Giorgi Iankoshvili, Elisabeth Karalashvili, Revaz Kvaratskhelia, Natia Rtskhiladze, Nutsa Rtskhiladze, Alisa Sanakoeva, Anano Shubashishvili, Irina Tsereteli and Mari Tsulaia. The traps were operating from April to November 2018. From the collected samples several taxa were then sorted out at ISU and prepared for further taxonomic research and DNA barcoding, using equipment purchased by the GIZ (Deutsche Gesellschaft für Internationale Zusammenarbeit; see below). Since the amount of collected material was very large, this work is still in progress and we are currently focusing on some selected groups of animals (several families of dipterans, hymenopterans, and beetles; spiders, pseudoscorpions and myriapods). The proximate goal is to evaluate multi-taxon species diversity and community structure over an elevation gradient. Furthermore, microclimate data logger stations registering air temperature, soil temperature, relative humidity and solar radiation were installed along the transect.





**Figs 1–9.** The Kintrishi Project. 1. Björn Rulik (ZFMK) and Levan Mumladze (ISU) with ISU students. 2. Malaise trap above the tree line (2500 m). 3. Björn Rulik and Ameli Kirse (ZFMK) teaching students at Grigoleti Research Field Station. 4. Grigoleti field station. 5. Traditional Georgian dinner prepared by local contractors from Grigoleti. 6. On the way to Kintrishi Protected Areas. 7. Just the “normal” way to work. 8. Bridge in Kintrishi Protected Areas. 9. Electrofishing in Kintrishi River.





**Figs 10–17.** Biodiversity Days 2018. **10.** Curious pigs examining fishing gear. **11.** Changing a flat tire on the way to work. **12.** Bakhmaro. **13.** Sceptical glance in Borjomi NP. **14.** Collecting calves?! (Borjomi NP). **15.** Hill top near Lentekhi. **16.** Traditional dinner in a private accommodation in Lentekhi. **17.** Between Lentekhi and Tsana.



Besides the Malaise trap transect two additional Malaise traps were set up: one was located next to the field station in Grigoleti for one week in April 2018. The other trap was set up close to the rangers' station in Kintrishi, who emptied the trap every other week, alternating with the ISU team. This trap was contributed by the Global Malaise Trap Program (GMP; <https://biodiversitygenomics.net/projects/gmp/>), which is run by the Centre for Biodiversity Genomics, University of Guelph, Canada. After the collecting season the material was sent to Guelph to obtain morphospecies-based barcode sequences.

In addition to Malaise trap sampling, soil samples have been collected along the elevation gradient to run a metabarcoding study of Nematoda diversity and pitfall traps were also set-up to sample ground beetle communities in the Kintrishi area.

In July 2018, a group of Georgian and German scientists, students and external taxon specialists (including citizen scientists) visited the Kintrishi Protected Areas to collect and identify specimens for DNA barcoding within so-called Biodiversity Days (i.e., a concerted, intense multi-taxon field sampling campaign, also referred to as a Bioblitz), the first so far to take place in Georgia. During the core dates (20–22 July) all participants were accommodated at the ISU field station in Grigoleti (Figs 4–5). During the days before and after these core days several groups of scientists also visited other areas of the country (e.g., the Greater Caucasus) to collect specimens (Appendix I: Table 1; Map (Fig. 56), Figs 12–21).

Apart from the pilot project funding by the BMBF (German Federal Ministry of Education and Research), the GIZ Georgia kindly supported this event under the Integrated Biodiversity Management South Caucasus (IBiS) initiative, funded by the BMZ (Federal Ministry for Economic Cooperation and Development). Collecting permits were provided by the Agency of Protected Areas of Georgia and the Ministry of Environment Protection and Agriculture of Georgia.

In addition to the students and scientists who were already involved into the Malaise trap project (listed above) the following researchers participated in the Biodiversity Days 2018: Cort Anderson (ISU), Jonas Astrin (ZFMK – Arthropoda), Ani Bikashvili (ISU – Mollusca), Tim Böhner (Uni Bonn – Botany), Albia Consul (ZFMK – herpetology, Arthropoda), Giorgi Epitashvili (ISU – Fishes), Marianne Espeland (ZFMK – Trichoptera, Lepidoptera), Matthias Geiger (ZFMK – Fishes), Nils Hein (Geographisches Institut der Universität Bonn – Arachnida), Hajo Krammer (ZFMK – Arachnida), Katharina Kurzrock (ZFMK – Mollusca), Ximo Mengual (ZFMK – Diptera), Stefan Otto (independent researcher – Arachnida), André Reimann (GBOL team; Senckenberg Naturhistorische Sammlungen Dresden – Diptera, Scorpiones), Anke Schäfer (GBOL team; independent researcher – Diptera, Botany), David Tarkhnishvili (ISU – herpetology), Birthe Thormann (ZFMK – Coleoptera), Jana Thormann

(ZFMK – Arthropoda), Sönke Twietmeyer (GBOL team; Nationalpark Eifel – Aves, Mammalia), Thomas Wesener (ZFMK – Myriapoda), Benedict Wipfler (ZFMK – Coleoptera).

Combining morphological and molecular data for species investigations, the collecting efforts in 2018 resulted in the submission of a first publication, which gives an updated list of the hoverflies (Diptera, Syrphidae) of Georgia (Mengual et al., submitted). This collaboration of Georgian students and external taxon specialists contributes to the species inventory and DNA barcoding reference library and is an example of the successful cooperation between ISU, ZFMK and external researchers.

## BIODIVERSITY DAYS 2019: THE GREATER CAUCASUS

After the successful trip to the Kintrishi area, the Biodiversity Days 2019 took place in the Stepantsminda area (Kazbegi) in the Greater Caucasus. During the core dates (4–7 July 2019) the participants were hosted at the ISU field station in Stepantsminda and, as in the previous year, small groups of scientists also collected in other regions of the country (e.g., Vashlovani National Park) before and after the core dates (Appendix II: Table 2, Map (Fig. 56), Figs 22–40).

Three Malaise traps were run during a few days around the core dates. In addition, yellow pan, light, pitfall and banana traps were used, as well as Winkler extractors for sifted leaf litter.

In addition to sampling described above, collecting of Heteroptera was done in a variety of habitats, with a focus on brachypterous species of subalpine meadows. So far, two Caucasian endemics have already been identified, one of them just recently described as new to science: *Scirtetellus gudali* Kiritshenko, 1951 and *Myrmecophyes (Plumiger) tomi* Konstantinov & Simov, 2018 (Fig. 54) (both Heteroptera: Miridae).

A quick scan through malaise material collected in Stepantsminda revealed specimens from at least 13 families of lower Diptera. Within the family Mycetophilidae (fungus gnats) the following discoveries are worth mentioning: a big series (14 ♂♂, 11 ♀♀) of *Coelosia flava* (Staeger, 1840), a typical boreo-montane faunal element (Fig. 55) and two females of the widespread but rarely collected species *Grzegorzekia collaris* (Meigen, 1818). Both species records represent the first proof for the Caucasus region.

At least 48 different mollusk species belonging to 24 families were recorded during the core event in Stepantsminda and a short trip from Tbilisi to Kutaisi 1–3 July 2019. Aside from more widespread Western Palearctic species and species occurring also in Anatolia, 16 species endemic to the Caucasus region were recorded. Especially noteworthy are three slug species: the first, *Svanetia*





**Figs 18–26.** The Greater Caucasus. **18.** Road to Tsana. **19.** Kiosk in Tsana. **20.** Searching for spiders. **21.** Collecting in Tsana, Greater Caucasus (1760 m a.s.l.). **22.** Malaise trap in the garden of Stepantsminda field station. **23.** View from field station to Mount Kazbek (5054 m) and Gergeti Trinity Church. **24.** Gergeti Trinity Church. **25.** View to Stepantsminda from Gergeti Trinity Church. **26.** After field work.



*caucasica* (Simroth, 1898), is a short-range endemic that is only known from the Kazbegi region and was recorded at the Jvaris Pass. The second is an unidentified species of the genus *Gigantomilax* that was collected north of Gergeti. The genus has previously not been recorded from the Kazbegi region. The third species, *Boettgerilla pallens* Simroth, 1912, is only known from western Georgia, where it was only rarely recorded in the past.

The following Georgian and German researchers attended the Biodiversity Days in Stepantsminda: Cort Anderson (ISU), Ulrich Burkhardt (Senckenberg Museum für Naturkunde Görlitz – Collembola), Marianne Espeland (ZFMK – Trichoptera, Lepidoptera), Matthias Geiger (ZFMK – Fishes, Macrozoobenthos), Nils Hein (Geographisches Institut der Universität Bonn – Arachnida), Kai Heller (GBOL team, independent researcher – Diptera), Bella Japoshvili (ISU – Fishes), Elisabeth Karalashvili (ISU – Arachnida), Thorsten Klug (ZFMK – Myriapoda), Hajo Krammer (ZFMK – Arachnida), Christiane Lange (independent researcher – Diptera), Cornelia Löhne (Uni Bonn – Botany), Peter Manko (University of Presov – aquatic Insects), Dirk Mattern (GBOL team, independent researcher – Trichoptera), Ximo Mengual (ZFMK – Diptera), Carsten Morkel (GBOL team, independent researcher – Heteroptera), Levan Mumladze (ISU), Marco T. Neiber (CeNak Hamburg – Mollusca), André Reimann (GBOL team; Senckenberg Naturhistorische Sammlungen Dresden – Diptera, Scorpiones), Dirk Rohwedder (ZFMK – Hymenoptera), Anke Schäfer (GBOL team; independent researcher – Diptera, Botany), Axel Ssymank (Bundesamt für Naturschutz Bonn – Diptera, Botany), Eckart Stolle (ZFMK – Hymenoptera), Jens-Hermann Stuke (GBOL team, independent researcher – Diptera), David Tarkhnishvili (ISU – herpetology), Jana Thormann (ZFMK – Arthropoda), Karin Voigtländer (Senckenberg Museum für Naturkunde Görlitz – Myriapoda), Benedict Wipfler (ZFMK – Coleoptera), Joachim Ziegler (Museum für Naturkunde Berlin – Diptera).

During the core dates several ISU students joined the researchers: Eka Arsenashvili, Giorgi Bananashvili, Ani Bikashvili, Tinatin Chkhartishvili, Sandro Chubinidze, Giorgi Epitashvili, Giorgi Iankoshvili, Shota Japarashvili, Giorgi Khubashvili, Giorgi Kirtkitadze, Revaz Kvaratskhelia, Natia Rtskhiladze, Nutsa Rtskhiladze, Alisa Sanakoeva, Anano Shubashishvili, Mariam Todua, Ana Tsertsvadze, Mariam Tsulaia and Mariam Zazadze.

According to their field of interest, the students accompanied the scientist during their work in the field and got training in different collecting methods and taxonomic identification.

An additional team of international scientists made an additional expedition one month earlier: Ximo Mengual (ZFMK), Sander Bot (Haren, Netherlands), Jeffrey H. Skevington (Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food

Canada, Ottawa, Canada), Frank Van de Meutter (Engsborgen, Belgium), Jeroen van Steenis (Naturalis Biodiversity Center, Leiden, Netherlands) and Lenze Hofstee (Haren, Netherlands) collected Diptera in different parts of Georgia 8–23 June 2019.

Furthermore, a joint excursion of students from the Geography department of the University of Bonn (GIUB), the ZFMK and the ISU was held in July/August 2019. This event aimed at teaching knowledge on the underlying mechanisms of the high biodiversity in Georgia to students with different backgrounds.

## OUTLOOK

As a continuation of the work in GGBC, we currently plan a Georgian-Armenian-German initiative to establish a joint Caucasus Biodiversity Research Initiative, the Caucasus Barcode of Life Platform (CaBOL). The planned improvements of research and training infrastructure in a long-term international collaboration will provide the latest technology in molecular biodiversity research to Georgian and Armenian scientists and students. A strong initial focus of the project will lie in expanding the DNA barcoding reference databases for Georgia, as initiated within GGBC, and Armenia. CaBOL will collect DNA barcodes, and archive DNA, tissue samples and voucher specimens of Caucasian biodiversity, to the benefit of collections in Georgia, Armenia and Germany. The DNA barcodes and their metadata will be publicly available in a centrally managed database, and will be used for cooperative research projects by Georgian, Armenian and German scientists and students. Simultaneously, CaBOL will equip laboratories in Tbilisi (Georgia) and Yerevan (Armenia), with a strong hub at the Ilia State University, to train students from the South Caucasus region and beyond. Currently, there are no advanced biotechnology facilities available for non-medical research in Georgia and Armenia. Beyond DNA barcoding, infrastructural improvements and its training mission, CaBOL will expand its methodological spectrum by remote sensing approaches and will include experienced forestry partners from the University of Göttingen (Chair of Forest Inventory and Remote Sensing).

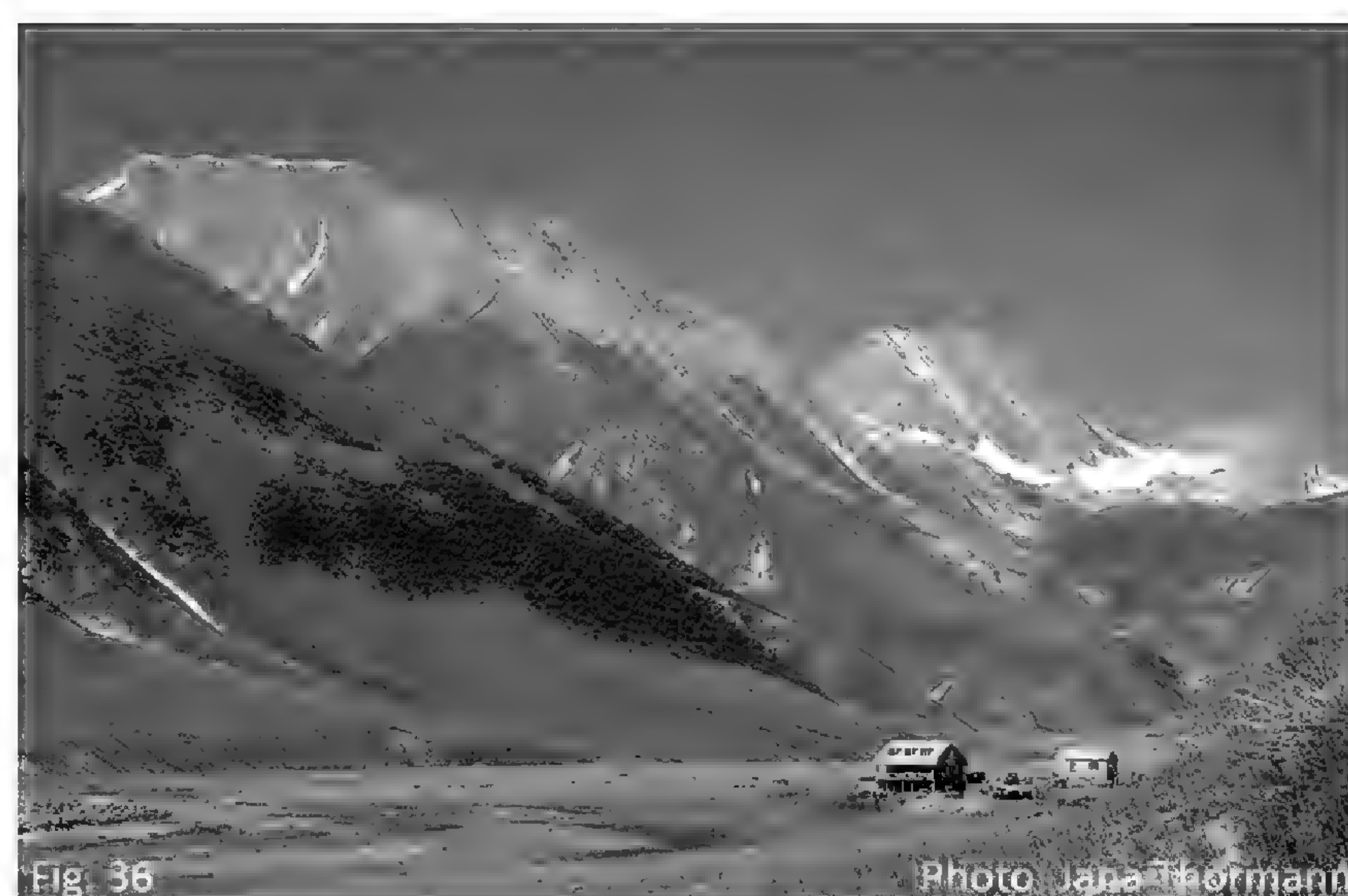
**Acknowledgements.** The GGBC-project was funded by the German Federal Ministry of Education and Research under grant number 01DK17048. The two field expeditions were supported by Deutsche Gesellschaft für Internationale Zusammenarbeit Georgia under the Integrated Biodiversity Management South Caucasus initiative, funded by the Federal Ministry for Economic Cooperation and Development (contract number 2018: 83291308, contract number 2019: 83322223). Collecting permits were kindly provided by the Agency of Protected Areas of Georgia and the Ministry of Environment Protection and Agriculture of Georgia. ZFMK kindly supported its employees





**Figs 27–34.** Biodiversity Days 2019. **27.** Analyzing dung samples. **28.** Winkler extractor in repurposed wardrobe. **29.** Daily way to work. **30.** Clearing the road. **31.** ISU students accompany scientists to the field. **32.** Analyzing soil samples in the field. **33.** Sno valley on the way to Juta. **34.** Juta and view to Chaukhi massif.





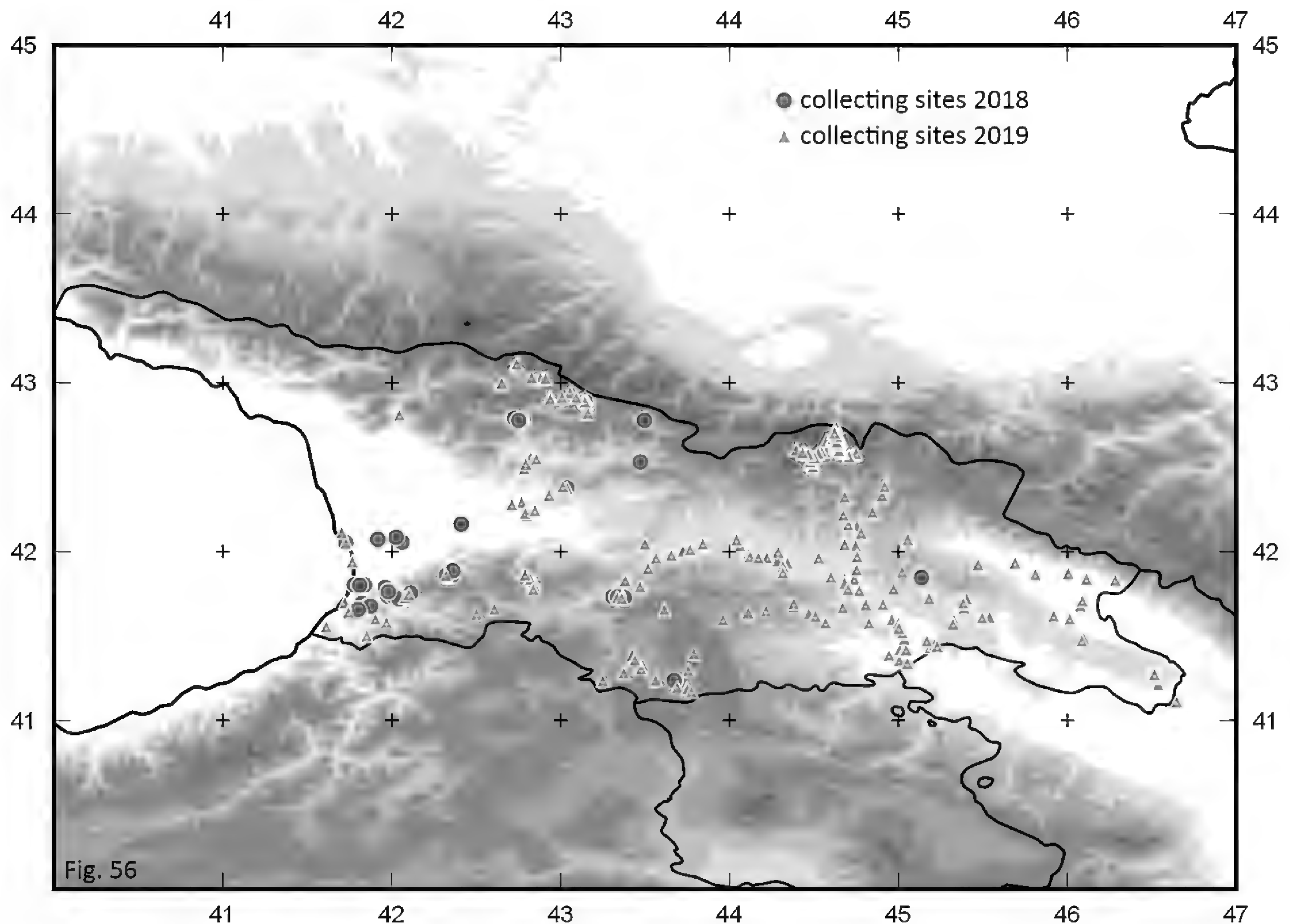
**Figs 35–42.** Various collecting sites. **35.** The fishing team. **36.** Truso gorge. **37.** View to Mna valley. **38.** Signaghi and Greater Caucasus in the background. **39.** Collecting on the way to Vashlovani Protected Areas. **40.** Vashlovani Protected Areas. **41.** Lesson in the field during joint excursion with Georgian and German students. **42.** Looking out for birds at Eagle Gorge near Dedoplistsqaro.





**Figs 43–55.** A snapshot of Caucasian biodiversity. **43.** Squamata: Viperidae, *Vipera dinniki* Nikolsky, 1913. **44.** Mecoptera: Panorpidae, *Panorpa communis* Linnaeus, 1758. **45.** Gastropoda: Hygromiidae, *Caucasigena eichwaldi* (Pfeiffer, 1846). **46.** Lepidoptera: Lycaenidae, *Polyommatus amandus* (Schneider, 1792). **47.** Coleoptera: Cerambycidae, *Rosalia alpina* (Linnaeus, 1758). **48.** Gastropoda: Limacidae, *Eumilax brandti* (Martens, 1880). **49.** Teleostei: Salmonidae, *Salmo ciscaucasicus* Dorofeyeva, 1967. **50.** Araneae: Atypidae, *Atypus muralis* Bertkau, 1890. **51.** Lepidoptera: Nymphalidae, *Melanargia russiae* (Esper, 1783). **52.** Diptera: Syrphidae, *Epistrophe leiophthalma* (Schiner & Egger, 1853). **53.** Diptera: Rhinophoridae, *Stevenia fausti* (Portshinsky, 1875). **54.** Heteroptera: Miridae, *Myrmecophyes tomi* Konstantinov & Simov 2018. **55.** Diptera: Mycetophilidae, *Coelosia flava* (Staeger, 1840).





**Fig. 56.** Map of collecting sites.

with logistics, equipment and travel expenses. We are thankful to all participants of the Biodiversity Days for collecting, identifying and providing specimens for further molecular analysis and thus helping to establish a reference database. We also thank the Georgian students who supervised the Malaise traps in Kintrishi and who are sorting the material.

## REFERENCES

- APA (2019) Agency of Protected Areas of Georgia. <https://apa.gov.ge/en/protected-areas/cattestone/kintrishis-daculi-teritoriebis-administracia>. Accessed 03/11/2019
- Astrin JJ, Höfer H, Spelda J, Holstein J, Bayer S, Hendrich L, Huber BA, Kielhorn KH, Krammer HJ, Lemke M, Monje JC, Morinière J, Rulik B, Petersen M, Janssen H, Muster C (2016) Towards a DNA Barcode Reference Database for Spiders and Harvestmen of Germany. *PLoS ONE* 11(9): e0162624. <https://doi.org/10.1371/journal.pone.0162624>
- Denk T, Frotzler N, Davitashvili N (2001) Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia Transcaucasia. *Biological Journal of the Linnean Society* 72: 287–332
- Garstecki T (2017) Feasibility assessment for a World Heritage nomination of the Colchic Forests and Wetlands under the natural criteria. Greifswald, Germany: pp. 132
- Geiger MF, Astrin JJ, Borsch T, Burkhardt U, Grobe P, Hand R, Hausmann A, Hohberg K, Krogmann L, Lutz M, Monje C, Misof B, Morinière J, Müller KF, Pietsch S, Quandt D, Rulik B, Scholler M, Traunspurger W, Haszprunar G, Wägele W (2016) How to tackle the molecular species inventory for an industrialized nation – lessons from the first phase of the German Barcode of Life initiative GBOL (2012–2015). *Genome* 59(9): 661–670. <https://doi.org/10.1139/gen-2015-0185>
- Hebert PDN, Cywinska A, Ball SL, Dewaard J (2003a). Biological identification through DNA barcodes. *Proceedings of the Royal Society of London B* 270: 313–321
- Hebert PDN, Ratnasingham S, DeWaard JR (2003b) Barcoding animal life: Cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society of London B* 270: S596–S599
- Kikvidze Z, Ohsawa M (1999) Adjara, East Mediterranean refuge of Tertiary vegetation. Pp. 297–315 in: Ohsawa M, Wildpret W, Arco MD (eds) *Anaga Cloud Forest, a comparative study on evergreen broad-leaved forests and trees of the Canary Islands and Japan*. Chiba University Publications
- Milne RI, Abbott RJ (2002) The origin and evolution of Tertiary relict floras. *Advances in Botanical Research* 38: 281–314
- Mittermeier RA, Gil PG, Hoffmann M, Pilgrim J, Brooks T, Mittermaier CG, Lamoreux J, da Fonseca GAB (2004) *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. CEMEX/Agrupacion, Sierra Madre
- Morinière J, Hendrich L, Balke M, Beermann AJ, König T, Hess M, Koch S, Müller R, Leese F, Hebert PDN, Haus-



mann A, Schubart CD, Haszprunar G (2017) A DNA barcode library for Germany's mayflies, stoneflies and caddisflies (Ephemeroptera, Plecoptera and Trichoptera). *Molecular Ecology Resources* 17: 1293–1307. <https://doi.org/10.1111/1755-0998.12683>

Mumladze L, Japoshvili B, Anderson EP (2019) Faunal Biodiversity Research in the Republic of Georgia: A Short Review of Trends, Gaps, and Needs in the Caucasus Biodiversity Hotspot. *Preprints* 2019, 2019080249. <https://doi.org/10.20944/preprints201908.0249.v1>

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858

Neidze V (2003) *Sakartvelos sotsialur-ekonomikuri geografia* (Social-economic geography of Georgia). Metsniereba, Tbilisi, Georgia

Raupach MJ, Hendrich L, K  chler SM, Deister F, Morini  re J, Gossner MM (2014) Building-Up of a DNA Barcode Library for True Bugs (Insecta: Hemiptera: Heteroptera) of Germany Reveals Taxonomic Uncertainties and Surprises. *PLoS ONE* 9(9): e106940. <https://doi.org/10.1371/journal.pone.0106940>

Rulik B, Eberle J, von der Mark L, Thormann J, Jung M, K  hler F, Apfel W, Weigel A, Kopetz A, K  hler J, Fritzlar F, Hartmann M, Hadulla K, Schmidt J, H  rren T, Krebs D, Theves F, Eulitz U, Skale A, Rohwedder D, Kleeberg A, Astrin JJ, Geiger MF, W  gele JW, Grobe P, Ahrens D (2017) Using taxonomic consistency with semi-automated data pre-processing for high quality DNA barcodes. *Methods in Ecology and Evolution* 8(12): 1878–1887. <https://doi.org/10.1111/2041-210X.12824>

Shatilova I, Mchedlishvili N, Rukhadze L, Kvavadze E (2011) *The History of the Flora and Vegetation of Georgia* (South Caucasus). Georgian National Museum, Institute of Paleobiology, Tbilisi

Tarkhnishvili D, Gavashelishvili A, Mumladze L (2011) Palaeoclimatic models help to understand current distribution of Caucasian forest species. *Biological Journal of the Linnean Society* 105(1): 231 –248

Wesener T, Voigtl  nder K, Decker P, Oeyen JP, Spel-da J, Lindner N (2015) First results of the German Barcode of Life (GBOL) – Myriapoda project: Cryptic lineages in German *Stenotaenia linearis* (Koch, 1835) (Chilopoda, Geophilomorpha). *ZooKeys* 510: 15–29. <https://doi.org/10.3897/zookeys.510.10176>

Zazanashvili N, Sanadiradze G, Bukhnikashvili A, Kandaurov A, Tarkhnishvili D (2004) Caucasus. Pp. 148–153 in: Mittermeier RA, Gil PG, Hoffmann M, Pilgrim J, Brooks T, Mittermaier CG, Lamoreux J, da Fonseca GAB (eds) *Hotspots revisited, Earth's biologically richest and most endangered terrestrial ecoregions*. CEMEX/Agrupacion, Sierra Madre.

APPENDIX II.

Table 1. Collecting sites of 2018, Georgia.

Locality description	Latitude	Longitude	Altitude	Collection date
1 km N of Bakhmaro	41.8576	42.3237	2055 m	19.07.18
Barkhmaro	41.8576	42.3240	2050 m	19.07.18
Black Sea coast near Grigoleti in front of Ilia University field station	42.0535	41.7260		19.07.18
Borjomi, pipeline road between Sakire and Tsikhisjvari, 0.65 km V of Kodiani, meadow and open pine tree forest with large amounts of perennial herbs	41.7271	43.3773	1863 m	22.07.18
Borjomi, pipeline road between Sakire and Tsikhisjvari, 1.75 km W of Kodiani, drier meadow with flowers	41.7323	43.3221	1772 m	23.07.18
Borjomi, pipeline road between Sakire and Tsikhisjvari, 2.3 km E of Sakire, dryish meadow with some wetter areas	41.7325	43.3068	1552 m	22.07.18
Borjomi, pipeline road between Sakire and Tsikhisjvari, 2.9 km E of Kodiani, very diverse meadows	41.7272	43.3771	2190 m	23.07.18
Bugdasheni river, near small Arakali	41.2356	43.6720		01.11.18
Chkhakoura – Bakhmaro road	41.8607	42.3574	1935 m	19.07.18
Chkhakoura – Bakhmaro road, 2.9 km ENE of Bakhmaro, overgrazed meadows	41.8610	42.3569	1900 m	19.07.18
Ghebi	42.7774	43.4956	1410 m	17.07.18
Grassy peak 1 km N of Bakhmaro	41.8611	42.3237	2192 m	19.07.18
Grigoleti, Ilia State Universtity Marine Biological Station	42.0529	41.7272	0 m	18.–20.07.18
Iori River, down from the Paldo Dam	41.8465	45.1357		23.06.18
Khino , entrance	41.7637	41.9788	385 m	27.07.18
Kintrishi	41.7369	41.9839		21.07.18
Kintrishi	41.7520	41.9760	451 m	21.07.18
Kintrishi	41.7880	41.9630		21.07.18
Kintrishi	41.7370	41.9810		21.07.18
Kintrishi drainage: Kintrishi River downstream of old bridge	41.7889	41.9603		21.07.18
Kintrishi drainage: Kintrishi River in Kobuleti Village, upstream of railway bridge	41.8033	41.7778		21.07.18
Kintrishi drainage: Kintrishi River near village Kveda Sameba	41.7991	41.8480		21.07.18



Table 1. Continued.

Locality description	Latitude	Longitude	Altitude	Collection date
Kintrishi drainage: Kintrishi River SE of Khutsubani Village	41.8029	41.8384		20.07.18
Kintrishi drainage: Kintrishi River, upstream of gravel quarry E of Kobuleti	41.8016	41.8095		22.07.18
Kintrishi National Park, at bisection behind ranger station; under bark and dead wood relatively close to the river; humid leaf litter	41.7303	41.9817	450 m	20.07.18
Kintrishi Nature Reserve	41.7345	41.9888	460 m	18.07.18
Kintrishi Nature Reserve, Khino	41.7380	42.0076	595 m	18.07.18
Kintrishi Nature Reserve, Khino	41.7345	41.9888	980 m	20.07.18
Kintrishi NR	41.7369	41.9839	450 m	29.07.18
Kintrishi NR, Khino monastery	41.7286	42.0781		29.07.18
Kintrishi NR, picnic spot	41.7319	41.9753	570 m	21.07.18
Kintrishi Protected Areas	41.7621	41.9785	318 m	19.07.18
Kintrishi Protected Areas	41.7366	41.9787	415 m	19.07.18
Kintrishi Protected Areas	41.7349	41.9710	400 m	19.07.18
Kintrishi Protected Areas, Didvake	41.7463	42.0167	1102 m	18.07.18
Kintrishi Protected Areas, Didvake Village	41.7172	42.0467	800 m	17.07.18
Kintrishi Protected Areas, monastery at Khino, meadows	41.7287	42.0782	906 m	20.07.18
Kintrishi Protected Areas, monastery at Khino, meadows, meadow – pine forest mosaic	42.7752	42.7608	1370 m	25.07.18
Kintrishi River, side valley	41.7346	41.9758	670 m	19.07.18
Kintrishi, Khino	41.7287	42.0782	980 m	21.07.18
Kintrishi, National Park	41.7440	42.0832	1280 m	21.07.18
Kintrishi-National Park, woods and meadows around Khino Monastery	41.7169	42.0552		23.07.18
Kintrishi-National Park, wayside between Didvake and Khino along Kintrishi River	41.7173	42.0469	790 m	18.07.18
Near Lentekhi, antennae	42.7774	42.7502	1405 m	25.07.18
North from Atsana, along the road	42.0559	42.0594	275 m	19.07.18
Above Khino Church	41.7283	42.0841	1028 m	23.07.18
Above Khino Church, second meadow	41.7344	42.0845	1089 m	20.07.18
Paliastomi-Rioni drainage: Oragvisghele Stream SW of Lanchkhuti Village	42.0850	42.0246	–	19.07.18
Paliastomi-Rioni drainage: Swlana Stream S of Jurukveti Village, upstream of 02-18	42.0654	41.9209	–	24.07.18
Paliastomi-Rioni drainage: Swlana Stream W of Jurukveti Village	42.0783	41.9164	–	19.07.18
Paliastomi-Rioni drainage: Swlana Stream W of Jurukveti Village, upstream of 02-18	42.0730	41.9168	–	24.07.18
Rioni drainage: Gubistskali River E of Samtredia Town, above confluence with Rioni River and Rioni Channel	42.1625	42.4107	–	24.07.18
Road from Sakire to Tsikhisjvari	41.7303	43.3348	1910 m	22.07.18
Road from Sakire to Tsikhisjvari	41.7271	43.3773	2185 m	22.07.18
Road from Sakire to Tsikhisjvari	41.7326	43.3081	1600 m	22.07.18
Road to Barkhamro	41.8609	42.3572	1935 m	19.07.18
Road to Barkhamro	41.8863	42.3614	1645 m	19.07.18
Road to Chkhakoura - Bakhmaro road, 5 km NE of Bakhmaro, meadows on ridge along road	41.8863	42.3612	1660 m	19.07.18
Road to Khino, Kintrishi Protected Areas, 6 km WNW of monastery at Khino, sunny, exposed rock face along road	41.7376	42.0074	638 m	18.07.18
Road to Tsana	42.8739	43.1500	1600 m	24.07.18
Samtskhe-Javakheti, road from Sakire to Tsikhisjvari	41.7303	43.3348	1900 m	23.07.18
Tsana	42.8889	43.1430	1760 m	24.07.18
Tskhmori, Chalistskali Waterfall	42.5313	43.4709	1225 m	18.07.18
Below Khino, meadow	41.7195	42.0408	840 m	18.07.18
Western Meskheta Mountains	41.7553	42.1112	2280 m	09.08.18



Table 1. Continued.

Locality description	Latitude	41.9782	Altitude	Collection date
Malaise Trap, ranger station Kintrishi	41.7621	41.9785	318 m	Apr.–Nov. 2018
Malaise Trap Grigoleti field station	42.0528	41.7269	7 m	17.–25.04.18
Malaise Trap Transect Kintrishi #1	41.7294	42.0776	1035 m	20.04.– 05.11.2018
Malaise Trap Transect Kintrishi #2	41.7294	42.0775	1020 m	20.04.– 05.11.2018
Malaise Trap Transect Kintrishi #3	41.7296	42.0773	1031 m	20.04.– 05.11.2018
Malaise Trap Transect Kintrishi #4	41.7441	42.0834	1264 m	20.04.– 05.11.2018
Malaise Trap Transect Kintrishi #5	41.7434	42.0818	1252 m	20.04.– 05.11.2018
Malaise Trap Transect Kintrishi #6	41.7433	42.0841	1235 m	20.04.– 05.11.2018
Malaise Trap Transect Kintrishi #7	41.7371	41.9792	404 m	20.04.– 05.11.2018
Malaise Trap Transect Kintrishi #8	41.7378	41.9786	403 m	20.04.– 05.11.2018
Malaise Trap Transect Kintrishi #9	41.7378	41.9782	401 m	20.04.– 05.11.2018
Malaise Trap Transect Kintrishi #10	41.7479	42.0959	1697 m	24.04.– 05.10.2018
Malaise Trap Transect Kintrishi #11	41.7477	42.0951	1637 m	24.04.– 05.10.2018
Malaise Trap Transect Kintrishi #12	41.7482	42.0940	1634 m	24.04.– 05.10.2018
Malaise Trap Transect Kintrishi #13	41.7552	42.1125	2268 m	24.04.– 05.10.2018
Malaise Trap Transect Kintrishi #14	41.7553	42.1128	2280 m	24.04.– 05.10.2018
Malaise Trap Transect Kintrishi #15	41.7554	42.1129	2280 m	24.04.– 05.10.2018
Malaise Trap Transect Kintrishi #16	41.7625	42.1157	2465 m	24.04.– 05.10.2018
Malaise Trap Transect Kintrishi #17	41.7619	42.1162	2462 m	24.04.– 05.10.2018
Malaise Trap Transect Kintrishi #18	41.7616	42.1158	2450 m	24.04.– 05.10.2018



**APPENDIX II.****Table 2.** Collecting sites of 2019, Georgia.

Locality description	Latitude	Longitude	Altitude	Collection date
1.4 km WSW Ilmazlo	41.4240	45.0080	–	30.06.2019
10 km S. of Kasristskali, Vashlovani NR	41.2235	46.5353	390 m	10.07.2019
14 km E of Mestia	43.0254	42.8907	2550 m	13.06.2019
14.5 km E of Mestia, forest with <i>Rhododendron</i>	43.0284	42.8788	2345 m	13.06.2019
15 km E of Mestia	43.0266	42.9101	2860 m	13.06.2019
2 lakes between Amali River and Terek	42.7219	44.6225	1538 m	09.07.2019
2.8 km nnw Jikurebi Lake	41.5980	45.3260	–	01.07.2019
20 km S of Stepandsminda	42.5105	44.4949	2550 m	1.–7.7.2019
5 km W of Naduknari	42.0640	45.0636	1045 m	08.07.2019
7 km W of Ushguli, along the road	42.9179	42.9366	2290 m	16.06.2019
7 km W of Ushguli, hilltop	42.9062	42.9370	2615 m	16.06.2019
7.5 km N of Mestia, path to glacier	43.1017	42.7276	1850 m	14.06.2019
7.5 km N of Mestia, path to glacier	43.1133	42.7379	1800 m	14.06.2019
7.7 km NE Mele, meadow	42.8211	43.1607	1450 m	20.06.2019
Abastumani area, along path	41.8234	42.8400	2025 m	11.06.2019
Akavreta river, left tributary of Adjaristskali River	41.5821	41.9679	–	01.06.2019
Akhaldaba northeast of Borjomi, Nedzvi Sanctuary	41.9028	43.5167	890 m	15.07.2019
Akhaltsikhe, Snotskali River valley	42.5881	44.6667	1802 m	10.07.2019
Akhaltsikhe-Sno, Snotskali River valley	42.5997	44.6528	1780 m	10.07.2019
Aktas Golu	41.2360	43.2490	–	11.07.2019
Alazani Chanal, near Tibaani	41.6016	46.0139	–	22.05.2019
Alazani River, down from the Shilda	41.9351	45.6891	–	25.07.2019
Alazani River, tributary of Kabali – Alazani, Tsnori bridge	41.6807	46.0756	–	22.05.2019
Algeti River 0.8 km WNW Tskhrakudaani	41.6750	44.3790	–	10.07.2019
Algeti River 3.4 km NW Abrameti	41.6340	44.4690	–	13.07.2019
Algeti River N Partskhisi	41.5790	44.5670	–	13.07.2019
Almasiani, southern end of village	42.5544	44.4969	1990 m	07.07.2019
Along Khde River above Dariali Monastery complex, 10 km N of Stepanzminda; Kazbegi Municipality	42.7360	44.6341	1350 m	02.07.2019; 06.07.2019
Along path to Gveleti big waterfalls, rich, variable meadows, scree; Kazbegi Municipality	42.7053	44.6149	1450–1700 m	02.07.2019; 06.07.2019
Alpana towards Kutaisi, Rioni Valley, limestone cliff along road	42.5581	42.8206	380 m	02.07.2019
Alpana towards Kutaisi, Rioni Valley, right side, north of Mekvena	42.4914	42.7839	370 m	02.07.2019
Alpana towards Kutaisi, Rioni Valley, southern entrance of canyon-like part of valley	42.5219	42.7942	380 m	02.07.2019
Alpana, limestone cliffs on left side of Rioni Valley	42.5592	42.8486	420 m	02.07.2019
Ananuri towards Zhinvali Dam, ca 4.5 km along road north of the dam	42.1525	44.7531	940 m	03.07.2019
Ananuri, slope opposite monastery, beyond bridge	42.1606	44.7028	880 m	03.07.2019
Aragvi River NE Zhinvali	42.1120	44.7780	–	07.07.2019
Aragvi River W Bulachauri	42.0360	44.7460	–	07.07.2019
Aragvi River W Choporti	41.9730	44.7560	–	07.07.2019
Aragvi Valley, between junction towards Dgnali and Tsivtskaro	42.2175	44.6728	910 m	07.07.2019
Aragvi Valley, Bibiliani, southern end of village	42.3244	44.6814	1050 m	07.07.2019
Bakhmaro	41.8600	42.3200	2000 m	03.08.2019
Batumi, Botanical Garden	41.6990	41.7220	–	19.07.2019



**Table 2.** Continued.

Locality description	Latitude	Longitude	Altitude	Collection date
Mountain station at Kobi	42.5112	44.4929	2957 m	07.07.2019
Between Kanobi and Pkhelshe along river Kesia	42.5980	44.5410	–	07.07.2019
Between Kvishkheti and Khashuri	41.9625	43.5636	740 m	08.06.2019
Between Tianeti and Akhmeta	42.0640	45.0640	1000 m	08.07.2019
Between Tskneti and Kojori	41.6700	44.6690	–	15.07.2019
Blashoviskhevi River SW Norio	41.7800	44.9700	–	02.07.2019
Borjomi	41.8320	43.3820	–	28.07.2019
Bridge on road to Gveleti waterfalls, fast-flowing, rocky stream with a lot of vegetation around	42.7074	44.6247	1493 m	02.07.2019; 06.07.2019
Bughdasheni Lake	41.1980	43.6890	–	12.07.2019
Bursa Stream, tributary to Alasani River about 3 km S of Sanavardo	41.8670	45.8100	–	08.07.2019
Chargali, Pschawi-Aragwi	42.3342	44.9031	1029 m	05.07.2019
Charnali, Sarpi	41.5560	41.6110	–	19.07.2019
Chili-Chili River in Beshtasheni	41.6410	44.1090	–	13.07.2019
Chkheri River, Stepanzminda	42.6712	44.6123	2000 m	02.–03.07.2019
Chkheri Valley northwest of Stepanzminda	42.6708	44.6170	1960 m	05.07.2019
Chkheri Valley, right side	42.6706	44.6097	2030 m	04.07.2019
Chrami River N Tikilisa	41.5970	43.9600	–	13.07.2019
Cow and horse pasture W of Stepandsminda	42.6668	44.6303	1812 m	1.–7.7.2019
Daliari Valley	42.7371	44.6318	1319 m	08.07.2019
Dariali gorge	42.7030	44.6270	–	05.07.2019
Dariali Gorge, surroundings of the monastery complex of the Holy Archangels Michael and Gabriel	42.7362	44.6333	1340 m	
Debeda River E Kirach-Mughanlo	41.3340	45.0680	–	30.06.2019
Debeda River N Khanji-Gazlo	41.3570	45.0050	–	30.06.2019
Debeda River N Kirach-Mughanlo	41.3400	45.0510	–	30.06.2019
Debeda River W Didi Mughanlo	41.3890	44.9430	–	30.06.2019
Dedoplistskharo, road to Eagle Canyon, very dry meadow dominated by <i>Eryngium</i>	41.4875	46.0944	770 m	10.07.2019
Enguri Dam	42.8100	42.0450	–	04.08.2019
Entrance Vashlovani Nationalpark	41.2143	46.5368	380 m	10.07.2019
Fluvial plane Tergi = Terek	42.6532	44.6356	1733 m	04.07.2019
Forest	42.0644	45.0635	1059 m	08.07.2019
Former road, tunnel	42.6900	44.6357	1633 m	08.07.2019
Gelati Monastery, walls and stones along path on the southside of the monastery	42.2939	42.7683	420 m	01.07.2019
Gergeti Sameba, valley west of church	42.6628	44.6106	2150 m	04.07.2019
Gergeti, close to road to Gergeti Trinity Church	42.6669	44.6128	2175 m	13.07.2019
Gergeti, Ghkheri Valley	42.6700	44.6103	2103 m	13.07.2019
Gergeti, Ghkheri Valley	42.6708	44.6119	1900 m	18.07.2019
Gergeti, north of village	42.6669	44.6303	1830 m	04.07.2019
Gergeti, road to Gergeti Trinity Church	42.6720	44.6100	–	04.07.2019
Gergeti, valley S of Gergeti Trinity Church	42.6617	44.6156	2080 m	13.07.2019
Gergeti Trinity Church parking spot	42.6650	44.6143	2257 m	1.–7.7.2019
Goderdzi Pass	41.6330	42.5010	–	20.07.2019
Goderdzi Pass	41.6610	42.6070	–	19.07.2019



Table 2. Continued.

Locality description	Latitude	Longitude	Altitude	Collection date
Gori Castle, southern side of castle hill	41.9856	44.1086	620 m	03.07.2019
Gori, Stalin Park	41.9867	44.1136	600 m	03.07.2019
Grigoleti	42.0530	41.7280	–	28.07.– 03.08.2019
Group of trees near Vashlovani NP	41.2524	46.5188	465 m	10.07.2019
Gudauri, lift station	42.5105	44.4954	3000 m	07.07.2019
Gudauri Pass, at Tufa formations	42.5336	44.4750	2210–2230 m	11.07.2019
Gveleti	42.7071	44.6254	1500 m	04.07.2019
Gveleti	42.7215	44.6225	1900 m	09.07.2019
Gveleti Lakes; Kazbegi Municipality	42.7227	44.6238	–	
Gveleti north of Stepanzminda slopes near the Great waterfall	42.7047	44.6184	1620 m	04.07.2019; 07.07.2019
Gveleti north of Stepanzminda valley below the waterfalls	42.7061	44.6224	1520 m	03.07.2019; 07.07.2019
Gveleti Waterfalls	42.7044	44.6205	–	1.–7.7.2019
Gveleti Waterfalls	42.7070	44.6252	1483 m	04.07.2019
Gveleti Waterfalls	42.7078	44.6253	1478 m	12.07.2019
Gveleti, near small waterfall	42.7025	44.6194	1645 m	17.07.2019
Gveleti, small waterfall	42.7050	44.6150	1600 m	06.07.2019
Gveleti, way to waterfall	42.7060	44.6170	1700 m	06.07.2019
Gveleti Valley	42.7074	44.6247	1485 m	02.07.2019
Heretiskari, way to Signaghi	41.7110	46.0870	200 m	09.07.2019
Iori River 8.5 km SE Sagaredscho	41.6680	45.3880	–	01.07.2019
Iori River N Qaracop	41.6130	45.5390	–	01.07.2019
Iori River NE Sartichala	41.7230	45.1810	–	01.07.2019
Jandara Reservoir 1.6 km SE Jandari	41.4350	45.1870	–	02.07.2019
Jandara Reservoir 2.8 km SE Mzianeti	41.4510	45.2120	–	02.07.2019
Jandara Reservoir 4.7 km SE Mzianeti	41.4400	45.2280	–	02.07.2019
Junction of Kora River valley and Juta Valley, valley bottom, rich in succulents; Kazbegi Municipality	42.5627	44.7070	1830 m	05.07.2019
Juta	42.5720	44.7310	–	05.07.2019
Juta	42.5797	44.7431	2160 m	05.07.2019
Juta at Sno-Valley, village	42.5795	44.7459	–	05.07.2019
Juta Valley, Juta mountainside with rich meadows; Kazbegi Municipality	42.5800	44.7423	2100–2200 m	05.07.2019
Juta, brook above the village	42.5839	44.7486	2185 m	10.07.2019
Juta, slope	42.5796	44.7436	2148 m	09.07.2019
Juta, village border	42.5794	44.7433	2150 m	10.07.2019
Jutistskali River	42.5838	44.7484	2182 m	10.07.2019
Jutistskali Valley, right side, near confluence with Kora River	42.5622	44.7061	1860 m	05.07.2019
Jvari Monastery, along road east of the monastery	41.8403	44.7367	600 m	01.07.2019
Jvari Pass	42.5189	44.4669	2360 m	07.07.2019
Kapatadze Lake	41.5730	45.3220	–	01.07.2019
Kasbek Mountains 5.6 km W Stepanzminda	42.6590	44.5760	–	05.07.2019
Keda, Kveda Agara	41.6020	41.9020	–	19.07.2019
Khde-riverbed above Dariali-Monastery-complex	42.7360	44.6342	1360 m	02.07.2019
Khino, Kintrishi	41.7290	42.0780	–	30.–31.07.2019



**Table 2.** Continued.

Locality description	Latitude	Longitude	Altitude	Collection date
Khomisdziri, Pschawi-Aragwi	42.3880	44.9185	1070 m	05.07.2019
Khornabuji	41.4724	46.0847	780 m	10.07.2019
Khurtisi, meadows with tall-herbs and mountainside with shorter vegetation; Kazbegi Municipality	42.5994	44.5444	1980–2200 m	07.07.2019
Kintrishi	41.7490	42.1000	–	31.07.2019
Kirkhbulaki River e Qulalisi	41.3270	43.4840	–	11.07.2019
Kobi, near Kobi Pass	42.4983	44.4931	2760 m	14.07.2019
Kobi, near Kobi Pass	42.5047	44.4931	2860 m	14.07.2019
Kobi, near ski lift base station	42.5572	44.4975	1825 m	14.07.2019
Kobi Valley/ river Tergi= Terek	42.5809	44.4642	2009 m	07.07.2019
Kochki River S Epremovka	41.1890	43.7480	–	12.07.2019
Korolistavi, Mtirala	41.6420	41.7430	–	18.07.2019
Ksani river, near Mukhrani Village	41.9628	44.5265	–	30.06.2019
Kumisi Lake, S of Tbilisi	41.5770	44.8240	–	16.07.2019
Kura drainage: Aragvi River near Naoza	41.9720	44.7550	–	07.07.2019
Kura drainage: Pshavis Aragvi River near Tsiprani Village, upstream of Zhinvali reservoir	42.2340	44.8450	–	05.07.2019
Kura drainage: small unnamed tributary stream to Pshavis Aragvi River about 5 km N of Chargali village	42.3870	44.9180	–	05.07.2019
Kura River 1.2 km Nn Metekhi	41.9340	44.3420	–	09.07.2019
Kura River 1.3 km NNW Tedotsminda	42.0350	44.0620	–	08.07.2019
Kura River 1.5 km W Khtsisi	41.9800	43.6550	–	08.07.2019
Kura River 1.6 km E Ilmazo	41.4280	45.0430	–	30.06.2019
Kura River 1.9 km ESE Ilmazo	41.4180	45.0420	–	30.06.2019
Kura River 2 km S Karajalari	41.5990	44.9600	–	29.06.2019
Kura River 2.0 km ESE Ilmazo	41.4200	45.0440	–	30.06.2019
Kura River 2.3 km NNE Teliani	41.9480	44.2820	–	09.07.2019
Kura River 2.3 km W Mtskheta	41.8390	44.6800	–	07.07.2019
Kura River 6.6 km E Khidistavi	41.9600	44.2100	–	09.07.2019
Kura River 7.5 km E Khidistavi	41.9650	44.2200	–	09.07.2019
Kura River E Variani	42.0730	44.0400	–	08.07.2019
Kura River N Akhalsheni	42.0050	43.7230	–	08.07.2019
Kura River NW Akhalsopeli	42.0130	43.7650	–	08.07.2019
Kura River NW Dzegvi	41.8500	44.5990	–	07.07.2019
Kura River SE Gachiani	41.5780	44.9990	–	29.06.2019
Kura River SE Gori	41.9710	44.1210	–	09.07.2019
Kura River, Rustawi	41.5510	45.0100	–	29.06.2019
Kura valley 2.3 km W Akhalsheni	41.4870	45.0380	–	29.06.2019
Kura valley 2.7 km W Akhalsheni	41.4840	45.0340	–	29.06.2019
Kura valley SE Rustawi	41.5200	45.0230	–	29.06.2019
Kutaisi, Bagrati Cathedral	42.2775	42.7050	210 m	02.07.2019
Kutaisi, Botanical Garden	42.2792	42.7097	160 m	01.07.2019
Kveda Chkhutuneti	41.5020	41.8510	–	19.07.2019
lakes 3.4 km N Tsdo	42.7160	44.6240	–	03.07.2019
Mariini Canal 3.4 km N Jandari	41.4730	45.1670	–	02.07.2019



Table 2. Continued.

Locality description	Latitude	Longitude	Altitude	Collection date
Meadows with basaltic rocks; Kazbegi Municipality	42.5797	44.4700	2000–2300 m	07.07.2019
Mineral Springs, Baidara Valley north of Jvari Pass	42.5319	44.4722	2250 m	05.07.2019
Middle station, Kobi	42.5317	44.4934	2513 m	07.07.2019
Mna-Valley, W of Shevardeni	42.5800	44.4700	–	07.07.2019
Monastery Church	42.6648	44.6148	2169 m	03.07.2019
Monestry N of Stepandsminda	42.7362	44.6330	1899 m	1.–7.7.2019
Mountain pasture at road between Achmeta and Tianeti	42.0635	45.0641	1030 m	08.07.2019
Nadarbazevis Tba	41.9990	44.2870	–	10.07.2019
Nakerala Pass	42.3758	43.0372	1230 m	02.07.2019
Nakhshirgele towards Kutaisi, ca 200 m east of bridge over Tchishura River	42.2150	42.7983	130 m	01.07.2019
Nakhshirgele towards Kutaisi, ca 500 m along road to Broloskedi	42.2300	42.7908	150 m	01.07.2019
Narvani River, Kobi	42.5616	44.5102	1959 m	04.07.2019
Navenakhevi, forest near Navenakhevi Cave	42.2461	42.8469	300 m	02.07.2019
Near to Lagodechi NP	41.8335	46.2825	550 m	09.07.2019
Near Tsana, along the road	42.8887	43.1429	1757 m	18.06.2019
Near Tsana, along the road	42.9012	43.1422	1835 m	18.06.2019
Near Tsana, along the road	42.9160	43.1428	1975 m	19.06.2019
Near Tsana, meadow	42.8889	43.1430	1760 m	18.06.2019
Near Ushguli, close to river Inguri	42.9499	43.0719	2270 m	15.06.2019
Near Ushguli, path to glacier	42.9437	43.0539	2220 m	15.–17.06.2019
Near Ushguli, up to the ruins	42.9101	43.0070	2295 m	17.06.2019
Near Vashlovani NP	41.2636	46.5261	–	10.07.2019
NW of Stepanzminda	42.6710	44.6100	2050 m	04.07.2019
NW of Stepanzminda	42.6740	44.6330	2200 m	01.–07.07.2019
On the way to Sighnaghi, village Heretiskari, oak grove	41.7106	46.0870	215 m	–
on the way to Telawi	42.0605	45.0617	1555 m	–
E of Sno, alluvial forest	42.5996	44.6531	1781 m	10.07.2019
Ozero Zres	41.3880	43.4230	–	11.07.2019
Pass from Ushguli to Tsana	42.9140	43.0911	2575 m	18.06.2019
Pastures 1 km E Stepanzminda	42.6580	44.6600	–	06.07.2019
Pastures around Gergeti Trinity Church	42.6650	44.6150	–	06.07.2019
Path from Chkheri riverbed to road to Gergeti Trinity Church	42.6694	44.6119	2000– 2103 m	04.07.2019
Plain at Akhaltsikhe	42.5889	44.6657	1802 m	09.07.2019
Poti, Paliastomi Lake	42.1150	41.7030	–	29.07.2019
Rioni Valley, ca 1 km along road towards Ambrolauri	42.5489	42.8558	440 m	02.07.2019
Riverbed at Terek between Achkhota and Stepanzminda	42.6359	44.6285	1755 m	05.07.2019
Riverside W of Stepandsminda	42.6707	44.6097	2044 m	1.–7.7.2019
Road between Tianeti and Akhmeta, near road to Vedzebi, grassy meadow with some flowers, surrounded by mixed beech forest	42.0739	45.0536	1100 m	08.07.2019
Road from Abastumani to Sairme	41.7963	42.8444	1700 m	10.06.2019; 11.06.2019
Road from Abastumani to Sairme	41.7969	42.8439	1725 m	10.–11.06.2019
Road from Abastumani to Sairme	41.8385	42.8194	2260 m	10.06.2019
Road from Abastumani to Sairme	41.8643	42.7784	1830 m	10.06.2019; 11.06.2019



**Table 2.** Continued.

Locality description	Latitude	Longitude	Altitude	Collection date
Road from Abastumani to Sairme, near river	41.7773	42.8372	1386 m	10.–11.06.2019
Road from Abastumani to Sairme, small creek	41.8638	42.7890	1800 m	11.06.2019
Road from Sakire to Tsikhisjvari	41.7305	43.3343	1900 m	09.06.2019
Road from Sakire to Tsikhisjvari, hilltop and surroundings	41.7250	43.3606	2519 m	–
Road to Gergeti Trinity Church	42.6670	44.6140	2100 m	01.–07.07.2019
Road to Gergeti Trinity Church	42.6730	44.6160	2250 m	01.–07.07.2019
Road to Vashlovani National Park, 7km NW of gate, dry steppe	41.2742	46.5146	450 m	10.07.2019
Rustawi, lake close to Kura River	41.5490	45.0020	–	29.06.2019
S of Lakhushdi, meadow	42.9988	42.6501	1270 m	13.–14.06.2019
S of Lakhushdi, meadow	42.9990	42.6502	1270 m	13.–14.06.2019
S of Sioni	42.5960	44.5700	1900 m	07.07.2019
S of Stepanzminda	42.6370	44.6310	–	05.07.2019
Saguramo	41.8944	44.7521	551 m	21.06.2019
Satsire, southern outskirts of village	42.3350	42.9300	560 m	02.07.2019
Scrub and undergrowth near Sighnaghi	41.6128	45.9329	660 m	–
Sheep and horse pasture	42.6504	44.6514	1861 m	1.–7.7.2019
Shevardini > Truso Gorge	42.5914	44.4378	2100 m	15.07.2019
Shevardini > Truso Gorge, near Tufa formations	42.5828	44.4303	2132 m	15.07.2019
Side valley (Kora River) of Sno Valley	42.5637	44.7074	1845 m	05.07.2019
Sighnaghi	41.6210	45.9180	–	09.07.2019
Sighnaghi, surroundings of “Best Host”	41.6213	45.9180	727 m	10.–11.07.2019
Sioni	42.5963	44.5702	2000 m	07.07.2019
Slope at Chkheri riverbed near Gergeti Trinity Church	42.6722	44.6114	2070 m	04.07.2019
Small lake 2.0 km ENE Patara Gondra	41.3070	43.4750	–	11.07.2019
Small lake 2.2 km ENE Imera	41.6500	44.2150	–	10.07.2019
Small lake N Sulda	41.2820	43.3720	–	11.07.2019
Small oakwood	41.7102	46.0876	229 m	10.07.2019
Small river 1.6 km WSW Tokhliauri	41.7210	45.4030	–	01.07.2019
Small river valley SW Manglisi	41.6940	44.3790	–	10.07.2019
Small valley 1.1 km NE Abrameti	41.6200	44.5080	–	13.07.2019
Small valley 4.8 km SE Giorgitsminda	41.6960	45.3830	–	01.07.2019
Small valley near Kanobi at Kesia River	42.5975	44.5406	1925 m	07.07.2019
Sno, Snotskali River valley	42.5989	44.6500	1780 m	11.07.2019
Snotskali River 0.6 km NW Sno	42.6090	44.6330	–	04.07.2019
Snotskali River 0.6 km SE Achkhoti	42.6180	44.6240	–	03.07.2019
Snotskali River 0.8 km SE Sno	42.6000	44.6450	–	04.07.2019
Snotskali River SE Akhaltsikhe	42.5880	44.6670	–	04.07.2019
Soramula River 1.7 km ENE Agara	42.0470	43.8410	–	08.07.2019
Stepantsminda, station of Ilia State University	42.6550	44.6492	1830 m	04.07.2019
Stepanzminda	42.6530	44.6550	1800 m	02.07.2019
Stepanzminda	42.6535	44.6496	1823 m	03.–06.07.2019
Stepanzminda	42.6549	44.6495	1900 m	1.–7.7.2019
Stepanzminda	42.6581	44.6566	1900 m	06.07.2019
Stepanzminda	42.6641	44.6144	2163 m	07.07.2019
Stepanzminda	42.6656	44.6365	1797 m	03.07.2019



Table 2. Continued.

Locality description	Latitude	Longitude	Altitude	Collection date
Stepanzminda	42.6704	44.6096	2034 m	03.07.2019
Stepanzminda, along road to Ioane Natismcemeli Orthodox Church, overgrazed meadows with <i>Hippophae rhamnoides</i> ; Kazbegi Municipality	42.6523	44.6538	1860 m	2.07.2019.
Stepanzminda, cow and horse pasture W of Stepandsminda	42.6678	44.6316	1810 m	—
Stepanzminda, Elm Monastery	42.6575	44.6567	1950 m	17.07.2019
Stepanzminda, Gveleti	42.7161	44.6239	1400 m	09.07.2019
Stepanzminda, Gveleti, Tibistskali River	42.7047	44.6208	1540 m	12.07.2019
Stepanzminda, Gveleti, Tibistskali River	42.7078	44.6253	1480 m	12.07.2019
Stepanzminda, hilltop north of Gergeti Trinity Church	42.6753	44.6158	2250 m	—
Stepanzminda, Ilia State University field station	42.6548	44.6490	1820 m	12.07.2019
Stepanzminda, Kasbek mountain	42.6667	44.6008	2470 m	18.07.2019
Stepanzminda, near Snotskali River mouth	42.6367	44.6308	1750 m	16.07.2019
Stepanzminda, near village	42.6628	44.6394	1745 m	16.07.2019
Stepanzminda, parking bay on the way to the Gergeti Trinity Church	42.6669	44.6136	2120 m	—
Stepanzminda, pass to Gergeti Glacier	42.6588	44.5736	2900 m	05.07.2019
Stepanzminda, road to Gergeti Trinity Church	42.6678	44.6106	2160 m	18.07.2019
Stepanzminda, slope opposite pastures	42.6672	44.6292	1825 m	—
Stepanzminda, Snotskali River mouth	42.6369	44.6325	1760 m	16.07.2019
Stepanzminda, steep mountainside, flower-rich with some drier areas, flower-rich meadow on top; Kazbegi Municipality	42.6755	44.6130	1980–2400 m	04.07.2019
Stepanzminda, Tergi River	42.6519	44.6392	1740 m	15.07.2019
Stepanzminda, way to hilltop north of Gergeti Trinity Church	42.6725	44.6161	1900–2250 m	—
Streamcourse	42.6711	44.6118	1996 m	09.07.2019
Streamcourse to monastery	42.6706	44.6096	2023 m	09.07.2019
Street to Baisubani	41.8399	46.1121	300 m	09.07.2019
Sulfur springs at Dschari Pass	42.5346	44.4756	2216 m	11.07.2019
Surami Pass, eastern side	42.0472	43.4981	910 m	03.07.2019
Tabatskuri	41.6600	43.6130	—	23.07.2019
Coombe, river Tegi= Terek	42.6843	44.6362	1594 m	08.07.2019
Valley station, Kobi	42.5573	44.4976	1988 m	07.07.2019
Tba Bazalet'i	42.0440	44.6810	—	07.07.2019
Tba Khanjali	41.2390	43.5610	—	10.07.2019
Tba Mada	41.1710	43.7730	—	12.07.2019
Tba Paravani	41.3980	43.7870	—	13.07.2019
Tba Saghamo	41.2970	43.7540	—	12.07.2019
Tbilisi National Park	41.8808	45.0204	1270 m	22.06.2019
Tbilisi, Botanical Garden	41.6872	44.8056	470 m	07.07.2019
Tbilisi, Chilitba Lake	41.8150	44.6800	—	25.05.2019
Tbilisi, Dighomi	41.7780	44.7010	—	17.07.2019
Tbilisi, Dighomi, next to cemetery	41.7710	44.7670	—	17.07.2019
Tbilisi, Kakheti Highway/Aleksandre Tvalchrelidze I Turn, hotel garden	41.6892	44.9078	480 m	07.07.2019
Tedzami River 1.4 km NE Zemo Khandaki	41.9130	44.3160	—	09.07.2019
Tedzami River, tributary to Kura river, near Ertatsminda Village	41.8760	44.3144	—	30.06.2019
Telawi, Guest House LeNi	41.9152	45.4719	760 m	08.07.2019
Telawi, surroundings of hostel	41.9241	45.4701	685 m	08.07.2019



**Table 2.** Continued.

Locality description	Latitude	Longitude	Altitude	Collection date
Teliangkhevi River W Paldo	41.6110	45.4940	—	01.07.2019
Terek drainage: Narvani River at Kobi Village close to confluence with Terek River	42.5612	44.5093	—	04.07.2019
Terek drainage: Snostskali River near Akhaltsikhe Village	42.5940	44.6600	—	06.07.2019
Terek drainage: Snostskali River SE of Sno Village, small side channel of main channelized river	42.6003	44.6469	—	02.07.2019
Terek River 0.4 km W Pansheti	42.6350	44.6240	—	03.07.2019
Terek River 0.5 km S Kanobi	42.5850	44.5240	—	04.07.2019
Terek River 1.0 km WSW Stepanzminda	42.6530	44.6350	—	03.07.2019
Terek River 1.3 km SW Stepanzminda	42.6490	44.6340	—	03.07.2019
Terek River 1.6 km W Ukhati	42.5580	44.5020	—	04.07.2019
Terek Valley near confluence with Khde River, north of Dariali Monastery	42.7369	44.6314	1300 m	06.07.2019
Terek Valley, Darial Gorge, east of Tsdo	42.6936	44.6414	1560 m	05.07.2019
Terek Valley, Darial Gorge, near Gveleti	42.7036	44.6269	1480 m	05.07.2019
Terek Valley, Darial Gorge, south of Gveleti	42.7014	44.6283	1480 m	05.07.2019
Terek Valley, Gveleti Small Waterfall	42.7050	44.6147	1720 m	06.07.2019
Tkhilistskaro	41.8727	46.0050	337 m	09.07.2019
Tkibuli towards Ambrolauri, below Nakerala Pass	42.3869	43.0119	1110 m	02.07.2019
Truso Gorge at Terek	42.5797	44.4699	2023 m	07.07.2019
Truso Gorge, slope	42.5777	44.4647	2140–2212 m	07.07.2019
Truso Valley, flowery meadows and scree fields, 400 m E of Abano; Kazbegi Municipality	42.6039	44.3934	2180–2300 m	3.07.2019.
Truso Valley, steep mountain side with flowers and scree; Kazbegi Municipality	42.5869	44.4305	2130–2200 m	3.07.2019.
Tsdo Village	42.6928	44.6353	1750 m	17.07.2019
Tsdo, old road around the road tunnel	42.6900	44.6361	1620–1630 m	09.07.2019
Tsdo, small river valley close to the road tunnel	42.6842	44.6347	1600–1646 m	09.07.2019
Tsiprani, Pschawi-Aragwi	42.2345	44.8450	852 m	05.07.2019
Ughviri Lake	43.0319	42.8273	1905 m	13.06.2019
Ureki, Shekvetili	41.9410	41.7660	—	02.08.2019
Ushguli	42.9143	43.0077	2082 m	15.06.2019
Vachiani Lake	41.3600	43.4390	—	11.07.2019
Vashlovani NP, bungalows near border to Azerbaijan	41.1110	46.6470	—	26.–27.07.2019
Walk to Gveleti waterfall	42.7047	44.6204	1555 m	—
Way from Bakuriani to Borjomi	41.7940	43.4690	—	23.07.2019
Wetland N Kvakhvrel	41.9640	44.1700	—	09.07.2019